A LEAF BLADE ANATOMICAL SURVEY OF *MUHLENBERGIA* (POACEAE: MUHLENBERGIINAE)

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ABSTRACT

Muhlenbergia includes 151 species of mostly New World origin; 133 species are indigenous to North America [although many of these range to Central America (33) and South America (14)]; 38 species occur in Central America (a single species is endemic); 25 species occur in South America (10 are endemic); and only six endemic species are known to occur in southern Asia. No modern subgeneric classification within the genus exists and species relationships are not clear. An anatomical survey of the leaf blade as viewed in transverse section has provided a unique set of 16 characters to test previous hypothesized relationships. A cladistic analysis utilizing these 16 characters was performed on all but three species of *Muhlenbergia*. Based on this analysis *Muhlenbergia* appears to be divisible into three major anatomical groups corresponding to two subgenera (*M.* subg. *Muhlenbergia*, and *Trichochloa*) and two sections (*M.* sect. *Epicampes* and *Podosemum*) in *M.* subg. *Trichochloa*. Even though the presence of sclerosed phloem is an important apomorphy in the evolution of species in *Muhlenbergia* subg. *Trichochloa*, it appears to have evolved twice since it occurs in four other species. Our study suggests that in *Muhlenbergia* subg. *Muhlenbergia* the C_4 photosynthesis, PCK subtype was a single evolutionary event since these species occur as a clade or an uninterrupted grade in our phylogenetic analysis.

RESUMEN

Muhlenbergia incluye 151 especies originarias principalmente del Nuevo Mundo; 133 especies son nativas de Norteamérica [aunque muchas de ellas llegan a distribuirse hasta Centro y Sudamérica (33 y 14 respectivamente)]; 38 especies habitan en Centroamérica (sola una especie es endémica); 25 especies se encuentran en Sudamérica (10 son endémicas); y solamente seis especies endémicas se distribuyen por el sur de Asia. No existe una clasificación subgenérica moderna del género y las relaciones entre las especies no son claras. Un reconocimiento anatómico de las hojas en sección transversal ha proporcionado un conjunto único de 16 caracteres para probar las relaciones hipotéticas previas. Se llevó a cabo un análisis cladístico utilizando estos 16 caracteres de todas (excepto tres) las especies de *Muhlenbergia*. En base a este análisis *Muhlenbergia* parece ser divisible en tres grandes grupos anatómicos correspondientes a dos subgéneros (*M.* subg. *Muhlenbergia* y *Trichochloa*) y dos secciones (*M.* sec. *Epicampes* y *Podosemum*) en *M.* subg. *Trichochloa*. Aún cuando la presencia de floema esclerosado es una apomorfía importante en la evolución de las especies de *Muhlenbergia* subgénero *Trichochloa*, parece que ha evolucionado dos veces ya que se presenta en cuatro especies. Nuestro estudio sugiere que dentro de *Muhlenbergia* el subtipo de fotosíntesis C_4 PCK en las especies del subgénero *Muhlenbergia* fué un evento evolutivo sencillo, ya que estas especies aparecen como un clado o un grado ininterrumpido en nuestro análisis filogenético.

The subtribe Muhlenbergiinae (Poaceae: Chloridoideae: Eragrostideae) was first circumscribed by Pilger (1956) to include only species of *Muhlenbergia* Schreb. with narrow single-flowered spikelets, firm glumes often shorter than the awned lemmas, and cylindrical caryopses. In this same treatment Pilger recognized *Epicampes* J. Presl [=*Muhlenbergia* subg. *Trichochloa* A. Gray, *M.* sect. *Epicampes* (J. Presl) Soderstr.] in subtribe Sporobolinae Ohwi. Pilger further divided *Muhlenbergia* into eight sections: *Acroxis* (Trin.) Bush, *Bealia* (Scribn.) Pilg., *Cinnastrum* (E. Fourn.) Pilg., *Clomena* (P. Beauv.) Pilg., *Muhlenbergia*, *Podosemum* (Desv.) Pilg., *Pseudosporobolus* Parodi, and *Stenocladium* (Trin.) Bush,. Subsequent authors have agreed that Pilger's infrageneric treatment of *Muhlenbergia* was not particularly phylogenetically informative (Soderstrom 1967; Pohl 1969; Morden 1985; Peterson and Annable 1991). More recently the following six genera have been shown to share common ancestry and have been placed in the Muhlenbergiinae: *Bealia* Scribn., *Blepharoneuron* Nash, *Chaboissaea* E. Fourn., *Lycurus* Kunth, *Muhlenbergia*, and *Pereilema* J. Presl (Duvall et al. 1994; Peterson 2000; Peterson et al. 1995, 1997).

Many agrostologists have erected segregate genera to emphasize critical features of the large and diverse genus, *Muhlenbergia*. Desvaux (1810) recognized the genus *Podosemum*, based on the caespitose, open-panicled, and long-awned *M. capillaris*. Palisot de Beauvois (1812) described the genus *Clomena* based on the annual *M. peruviana*, and Presl (1830) described *Epicampes* based on *M. robusta*. Two relatives of the type species of the genus (*M. schreberi*), *M. glomerata* and *M. andina*, were given generic status by Link (1833) as *Dactylogramma* and by Thurber (1863) as *Vaseya*, respectively. Nuttall (1848) described the genus *Calycodon* based on the widespread and often important range grass, *M. montana*. The only other generic name given to a species presently placed in *Muhlenbergia* is *Crypsinna*, described by Fournier (1886) and based on *M. macroura*. Hitchcock's (1935) transfer of many of these segregate genera to *Muhlenbergia* has been followed by most American and European botanists. The morphological characters that delimit the genus are spikelets with single perfect florets and hyaline or membranous lemmas with three usually prominent veins. These characters are not at all unique within the Eragrostideae and seem to be possessed by about half of the genera in the tribe.

The morphological diversity within *Muhlenbergia* is tremendous. Annuals less than 2 cm tall (*M. depauperata*, *M. minutissima*, *M. peruviana*, *M. ramulosa*) are not uncommon and there are numerous strongly caespitose perennials over 2 m tall (*M. gigantea*, *M. mutica*, *M. robusta*). Rhizomes and/or stolons are found in 1/4 of the species and there is a single species (*M. dumosa*) that has a growth form similar to bamboos. Leaf blades can be flat, involute, or folded with a variety of pubescence types located on the abaxial and/or adaxial surface. All species of *Muhlenbergia* have open or contracted (spike-like) panicles with the branches generally re-branched. At maturity or anthesis, the angle of the branches spreading from the culm axis and the total width of the inflorescence are diagnostic characteristics used to separate the species. Pedicel orientation can vary from appressed or spreading, to nodding and reflexed from the branches, and the pedicels can be either round or flattened in cross section. Most species of *Muhlenbergia* have single-flowered spikelets although there are two species that are occasionally 2 or 3-flowered (*M. asperifolia* and *M. uniflora*). The lemma is perhaps the most critical structure, and its features such as length, presence or absence of an awn or mucro, pubescence type and location, shape, and color can all be used to differentiate among the species. The single lemma is 3-veined (1-veined in *M. palmirensis*) with a stout central vein and two lateral veins, although the lateral veins are sometimes very hard to discern with a good (20X) dissecting microscope. The caryopsis has a fused pericarp and is usually free from both the lemma and palea in most species of Muhlenbergia, however the length, shape and to lesser extent color are highly variable.

At last tally, *Muhlenbergia* consisted of 151 species (Peterson 2000). The distribution of *Muhlenbergia* is almost entirely New World where 133 species are indigenous to North America [although many of these range to Central America (33) and South America (14)]; 38 species occur in Central America (a single species is endemic); 25 species occur in South America (10 are endemic); and only six endemic species are known to occur in southern Asia. One obvious hypothesis is that the genus arose where it is most diverse today, i.e., northern Mexico/southwestern U.S., and has since radiated. For a dispersal event, the longer the distance from the place of origin, would in theory, lessen the chance of a successful introduction. Therefore, there are many species of *Muhlenbergia* in North America, fewer in Central America, even fewer in South America, and finally very few in Asia. So far, all ten species in the subtribe Muhlenbergiinae that have been investigated genetically (Peterson and Herrera A. 1995; Peterson and Morrone 1998; Peterson and Ortíz-Diaz 1998; Peterson et al. 1993; Sykes et al. 1997) exhibit a north to south migration pattern, including *Muhlenbergia torreyi* (Peterson and Ortíz-Diaz 1998).

All species of *Muhlenbergia* previously examined exhibit kranz (C_4) leaf anatomy, particularly the parenchyma sheath subtype which is common in species occupying the most arid regions (Brown 1977; Hattersley 1984; Hattersley and Watson 1992). Two main subtypes, NAD-ME (nicotinamide adenine dinucleotide co-factor malic enzyme) and PCK (phosphoenolpyruvate carboxykinase) have been found, verified by biochemical assay, to occur within *Muhlenbergia* (Gutierrez et al. 1974; Hattersley and Browning 1981; Brown 1977; Hattersley and Watson 1976, 1992). These two biochemical subtypes differ in their predominant C_4 acid that is transported from primary carbon assimilation tissue (usually the mesophyll) to the photosynthetic carbon reduction (PCR) tissue (kranz sheath = parenchyma bundle sheath) [see Hattersley and Watson 1992]. There usually is an associated anatomical structure in PCK-like species that is diagnostic, such as, a looser arrangement of chlorenchyma tissue continuous between adjacent vascular bundles. In typical NAD-ME species the chlorenchyma is tightly radiate and usually separated from one vascular bundle to the next by a column of colorless cells. These differences have historically been used to separate these two subtypes; however, it has been shown in *Enneapogon* Desv. ex P. Beauv., *Eragrostis* Wolf, *Eriachne* R. Br., *Panicum* L., *Pheidochloa* S. T. Blake, *Triodia* R. Br., and *Triraphis* R. Br. that these anatomically PCK-like genera are actually biochemically NAD-ME (Ohsugi et al. 1982; Prendergast et al. 1986, 1987).

The first major anatomical investigation of *Muhlenbergia* was done by Holm (1901) who looked at 10 species and was able discern three groups: woodland types (= *M.* subg. *Muhlenbergia*); dry, rocky mountain slopes [= *M.* subg. *Trichochloa*, sect. *Epicampes* and other species]; and *M. filipes* (= *M.* subg. *Trichochloa*, sect. *Podosemum*). Holm (1901) pointed out that from an anatomical view-point these characteristics might prove useful in dividing *Muhlenbergia* into sections or subgenera.

Schwabe (1948) later investigated 22 species of *Muhlenbergia* that occur in South America and found that they correspond to four major groups: hygrophytes or mesic species (= *M.* subg. *Muhlenbergia*), xerophytic annuals one, xerophytic annuals two (= *M.* subg. *Muhlenbergia*), xerophytic perennials, and psammophytic perennials (= *M.* subg. *Trichochloa*, sect. *Podosemum*). Schwabe (1948) also suggested that *Muhlenbergia* should be separated from the genera of Agrostideae and incorporated into the Eragrosteae.

On the basis of leaf blade transectional anatomy and morphology Soderstrom (1967) distinguished two subgenera in *Muhlenbergia*, *Muhlenbergia* and *Podosemum* (= *Trichochloa*, an older name), and divided *M.* subg. *Trichlochloa* into two sections, sect. *Podosemum* and sect. *Epicampes*. Soderstrom placed 46 species of *Muhlenbergia*, which have partially sclerosed phloem and caps of sclerenchyma associated with the primary vascular bundles, into *M.* subg. *Trichochloa*. *Muhlenbergia* sect. *Epicampes* was characterized as having a compound keel (midvein) composed of primary and secondary vascular bundles sunken in a confluent mass of thick-walled parenchyma, whereas *M.* sect. *Podosemum* had a simple midvein composed of a single primary vascular bundle with additional tertiary vascular bundles present (Soderstom 1967).

Two years later Pohl (1969) completed a revision of 12 closely related species that he believed to represent the entire *M.* subg. *Muhlenbergia* in North America. Principal differences among the species in this study were size of the bulliform cells, size and degree of radial orientation of the chlorenchyma, and the extent to which the chlorenchyma was organized into discrete units surrounding each vascular bundle. Using morphological characteristics of the rhizome (possession of very short internodes with imbricate scales) and leaf blade (thin, flat blades with low length/width ratios), Pohl distinguished these species from others in the genus. However, these same characteristics are seen in *M. californica*, a species of the mountains and valleys of southern California, and many other species common to the southwestern United States/Mexico.

Morden and Hatch (1987, 1996) investigated the anatomical and morphological variation within the *M. repens* complex, which consists of six species in North and South America. Anatomical data supported the placement of *M. squarrosa* (Trin.) Rydb. as a synonym of *M. richardsonis*, and supported the recognition of two varieties of *M. villiflora*.

Peterson et al. (1989) and Peterson and Annable (1991) investigated 29 annual species of *Muhlenbergia* and found 14 characters useful in distinguishing four major species groups. Species of group (1) had flat blades, two tertiary vascular bundles between primary vascular bundles, vascular bundles positioned on the median layer, distinctly radiate and compact chlorenchyma cells separating adjacent vascular bundles, and fan-shaped central bulliform cells. Species of groups (2, 3 & 4) shared three characteristics: 1) indistinctly or incompletely radiate and loosely arranged chlorenchyma cells, 2) chlorenchyma cells continuous between vascular bundles, and 3) shield-shaped central bulliform cells (= *M.* subg. *Muhlenbergia*).

More recently a biosystematic study investigating the anatomy of the *M. montana* complex (consisting of 15 species) has been completed (Herrera-Arrieta 1998; Herrera-Arrieta and Grant 1994). Herrera-Arrieta and Grant used 18 characters to differentiate among these species and found four major species groups. Important characters appear to be the central midrib structure (similar in size to the other primary vascular bundles or presence of a prominent central midvein), the depth of the adaxial and abaxial furrows, sclerenchymatous girder development between the parenchyma bundle sheath and the epidermis, and epidermal vestiture (glabrous or papillose).

Leaf anatomical characters within the Poaceae as viewed in transverse section have long been recognized as important diagnostic features used to determine systematic relationships, and have been critical in elucidating infrageneric relationships within *Muhlenbergia* (Herrera-Arrieta and Grant 1993; Holm 1901; Morden and Hatch 1987; Peterson 2000; Peterson and Annable 1991; Peterson et al. 1989; Pohl 1969; Soderstrom 1967). A preliminary summary of our anatomical analysis is presented in Peterson (2000) where two subgenera, *M.* subg. *Muhlenbergia* and subg. *Trichochloa*, and a possible third group, '*Clomena*' are recognized. In this current paper we will give a detailed summary of the anatomical features as viewed in cross section of 148 of the possible 151 species within *Muhlenbergia* and present a subgeneric hypothesis that most closely reflects a cladistic analysis of the data. This is the first anatomical survey of nearly all species within this large variable genus.

MATERIALS AND METHODS

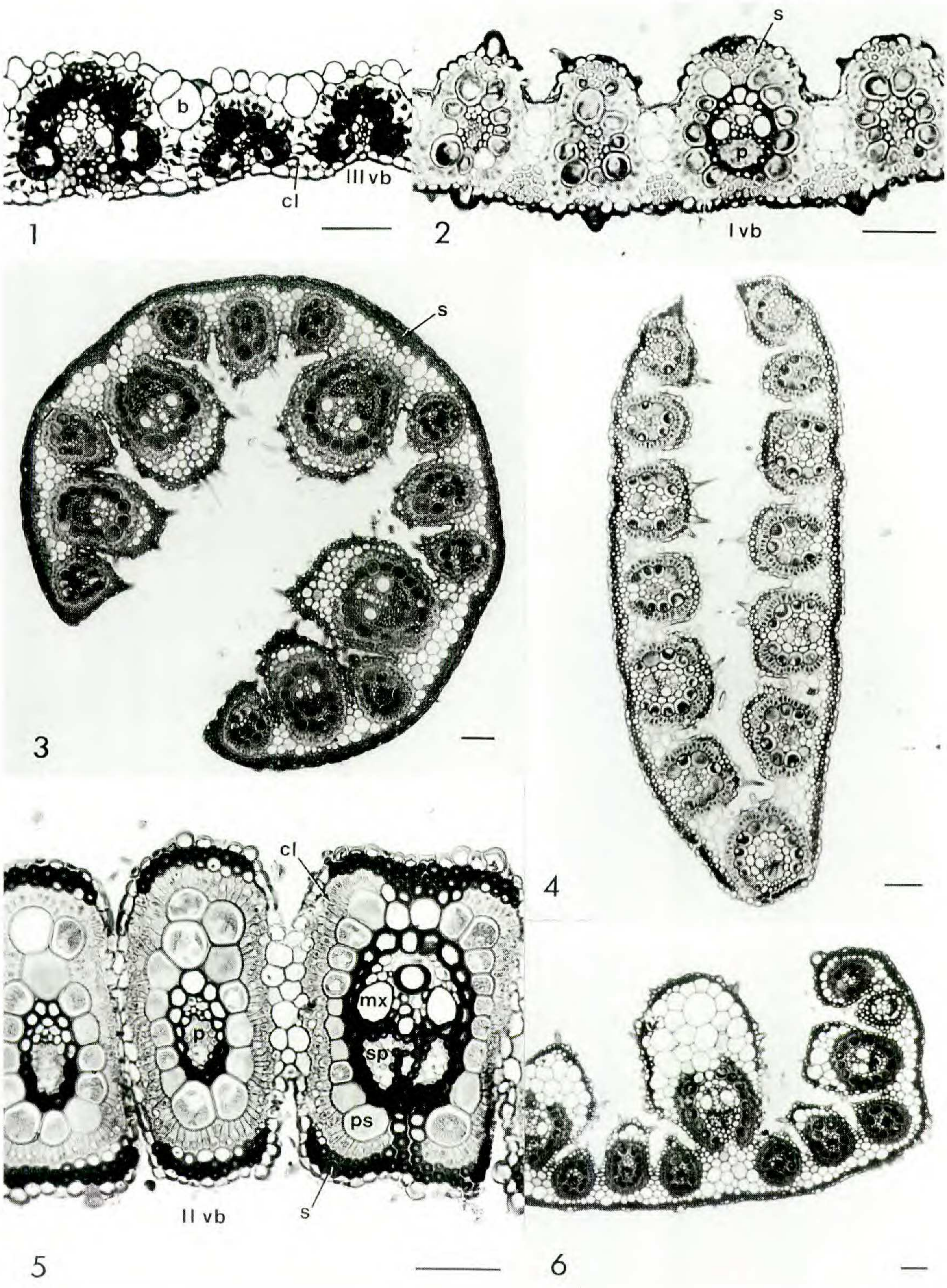
Over the last 16 years fresh field-collected leaf blades were obtained from North, Central, and South America, as well as China for anatomical study (Appendix 1). Five mm long leaf blade segments from the central third of the mid-culm region were fixed in FAA (10 parts EtOH; 1 part glacial acetic acid; 2 parts 37% formaldehyde; 7 parts distilled water). A few species (less than 5%) were studied from dried herbarium specimens because fresh field collected material was unavailable. Leaf blades were first desilicified in 100% hydrofluoric acid (HF) for 48 hours in order to ease microtomy, then dehydrated using 30, 50, 70, 90, 95, and 100% (twice) ethanol, graded into xylene (twice) and transferred to xylene: paraffin oil (1:1, steps 1 hour minimum). Blades were then dehydrated by using 2-2 dimethoxypropane (DMP), acetone, and tertiary butyl alcohol (TBA) series while in a vacuum. Infiltration was accomplished using two, six hour minimum changes of liquid paraffin before being embedded. The tissue was softened using 95% EtOH: Glycerin: HF (8:1:1) to improve slicing (Foster and Gifford 1947). A standard rotary microtome set at 6-10 :m thickness was used and sections were stained with safranin/fast green or 0.05% toluidine blue (Berlyn and Miksche 1976). Samples were examined and photographed on an Olympus BH-2 photomicroscope using Kodak TMAX black and white or Ektachrome color slide film.

Anatomical descriptions were completed following the procedure for standardizing comparative leaf anatomy in grasses as outlined by Ellis (1976). For purposes of comparison and standardization, primary vascular bundles (I°) are defined as containing large metaxylem elements on either side of the protoxylem elements with additional lysigenous cavities, and are usually associated with sclerenchyma girders or strands (Ellis 1976; Peterson et al. 1989). Secondary vascular bundles (II°) resemble 1° vascular bundles by having distinguishable xylem and phloem but lack large metaxylem elements and lysigenous cavitities. Tertiary vascular bundles (III°) contain indistinguishable xylem and phloem areas and are usually smaller than the I° and II° vascular bundles.

A list of the anatomical characters and their states used in all ensuing analyses appears in Table 1; a list of specimens used in this study is given in Appendix 1; and a complete data set is given in Appendix 2. The 153 taxon by 16 character data set was analyzed with WinClad2000. Parsimony heuristic analysis was performed with NONA (Goloboff 1998; Nixon 1999). We used 10 random taxon order replications in NONA, with TBR swapping holding 20 trees, followed by TBR swapping (to completion) holding up to 200 trees. A hard collapse of all unsupported nodes was selected to produce the cladogram in Figure 17. Since we were not testing for monophyly of the genus, the outgroup species were constrained, i.e., there were no synapomorphies supporting the *Muhlenbergia* clade.

TABLE 1. List of anatomical characters used in the cladistic analyses, their states, and comments.

1. **Adaxial furrow depth:** 1 = <1/5 blade thickness; 2 = 1/5-2/5 blade thickness; 3 = 1/2 or more than blade average thickness.
2. **Primary vascular bundle shape:** 1 = rounded; 2 = obovate/elliptic; 4 = rectangular. The overall outline is used to determine the shape. This includes the chlorenchyma and epidermis surrounding each vascular bundle.
3. **Vascular bundle outline size:** 1 = equal, primary vascular bundles about the same size as secondary and tertiary vascular bundles; 2 = subequal, secondary and tertiary vascular bundles 4/5 the size of primary vascular bundles; 3 = unequal, secondary and tertiary vascular bundles <2/3 the size of primary vascular bundles.
4. **Median (keel) vascular bundle structure:** 1 = simple keel, with only a single primary vascular bundle; 2 = compound keel, a single primary vascular bundle with only two additional tertiary vascular bundles; 3 = complex compound keel, with three or more additional primary, secondary, and/or tertiary vascular bundles. In state 1 there are no associated parenchyma cells, whereas state 2 and 3 have parenchyma cells involved in forming the compound keel.
5. **Vascular bundle position:** 1 = one level, centered at same level from adaxial to abaxial surface; 2 = two or three levels, usually closer to the abaxial surface.
6. **Vascular bundle composition:** 1 = with primary and secondary vascular bundles; 2 = with primary and tertiary vascular bundles; 3 = with primary, secondary, and tertiary vascular bundles. A primary vascular bundle (I°) contains two or more large metaxylem elements on either side of the protoxylem elements with additional lysigenous cavities and has distinguishable xylem and phloem. A secondary vascular bundle (II°) resembles a I° vascular bundle by having distinguishable xylem and phloem but lacks large metaxylem elements and lysigenous cavities. A tertiary vascular bundle (III°) contains indistinguishable xylem and phloem areas and is usually smaller than a I° and/or II° vascular bundle.
7. **Chlorenchyma arrangement:** 1 = radiate, compact; 2 = loosely arranged. State 1 corresponds with C_4 NAD-ME species where the chlorenchyma is not contiguous between each adjacent vascular bundle. State 2 corresponds with C_4 PCK species where the chlorenchyma is contiguous between each adjacent vascular bundle.
8. **Crown of inflated cells (adaxial) in primary vascular bundles:** 1 = absent; 2= present. The inflated areas are usually composed of parenchyma or collenchyma cells. In addition there may be sclerenchyma cells.
9. **Central bulliform cells shape:** 1 = circular- or irregular-shaped; 2 = almost fan-shaped to shield-shaped. State 2 is found when the bulliform cells do not form a complete column from the adaxial to the abaxial surface. In state 1 there is a column (contiguous between the adaxial and abaxial surface) of bulliform/colorless cells separating each adjacent vascular bundle.
10. **Number of secondary and/or tertiary vascular bundles between consecutive primary vascular bundles:** 1 = 1-3; 2 = 4 or more.
11. **Median vascular bundle structure:** 1 = not differentiated from other primary vascular bundles; 2 = differentiated from other primary vascular bundles.
12. **Median vascular bundle (abaxial) projection:** 1 = flattened, not enlarged; 2 = enlarged, bulbous with many strands of sclerenchyma.
13. **Sclerosed phloem in primary vascular bundles:** 1 = absent; 2 = present. State 2 is characterized by strands of sclerenchyma cells that divides the phloem.
14. **Sclerenchyma (adaxial) development in primary vascular bundles:** 1 = absent to a few fibers; 2 = one or two layers; 3 = three or more layers.
15. **Sclerenchyma (abaxial) development in the primary vascular bundles:** 1 = one or more layers, continuous along the width of the blade; 2 = one or more layers, discontinuous, only present below the vascular bundles; 3 = absent to a few fibers.
16. **Inflated cells (abaxial) in primary vascular bundles:** 1 = present; 2 = absent. The inflated areas are usually composed of parenchyma or collenchyma cells. In addition there may be sclerenchyma cells. This character is similar to number 8 but found on the abaxial surface.



FIGS. 1–6. Leaf blade anatomy of *Muhlenbergia*, adaxial surface uppermost in all photographs, except in 3 where the blade is involute. **1.** *M. ciliata* with shallow adaxial furrows (<1/5 leaf thickness), shallow abaxial grooves opposite the vascular bundles, loosely arranged chlorenchyma, only primary and tertiary vascular bundles present, and shield-shaped bulliform cells. **2.** *M. pauciflora* showing a flat lamina, medium adaxial furrows (1/5 – 1/3 leaf thickness), rounded primary vascular bundle shape, adaxial ribs opposite all vascular bundles, conic abaxial girder of sclerenchyma between each vascular bundle, vascular bundles centered in one level, unsclerosed phloem, sclerenchyma of only a few abaxial

All autapomorphies were not included in the final cladogram because they add no additional information for inferring relationships among two or more taxa.

RESULTS AND DISCUSSION

The results and discussion are interpreted in two parts: 1) a general description combining all species of *Muhlenbergia*, and 2) results of the cladistic analysis.

General Description of Leaf Structure.—Lamina (blades) are sometimes undulating, to more commonly flat, outwardly bowed, less commonly involute (Fig. 3), or folded (Fig. 4.). The angle formed by the two arms is broadly V or U shaped to expanded, occasionally loosely involute. Adaxial furrow depth in comparison to the leaf thickness can be slight, shallow (< 1/5 leaf thickness, Figs. 1, 11, 16), medium (1/5 to 1/3 leaf thickness, Figs. 2, 13), or deep (1/2 leaf thickness, Figs. 3, 10), and in the form of clefts located between all vascular bundles. Adaxial ribs are commonly present opposite all vascular bundles (Fig. 2), the same size to generally smaller than abaxial ribs, to less frequently absent with shallow groves opposite the vascular bundles (Fig. 1). Primary vascular bundle shape varies from rounded (Figs. 2, 4), to obovate/elliptic (Figs. 3, 6, 10) or rectangular (Figs. 5, 13, 14); secondary and tertiary vascular bundles also exhibit the same variation in shape. The secondary and tertiary vascular bundles are generally of the same size as the primary vascular bundles (Fig. 4), to about 4/5 the size of the primary vascular bundles (Fig. 5), or very unequal, less that 2/3 the size of the primary vascular bundles (Fig. 6). Abaxial projection of the median vascular bundle or midrib caused by sclerenchyma is sometimes large and with a protruding ridge (Fig. 7), to inconspicuous, often flat to round (Fig. 4).

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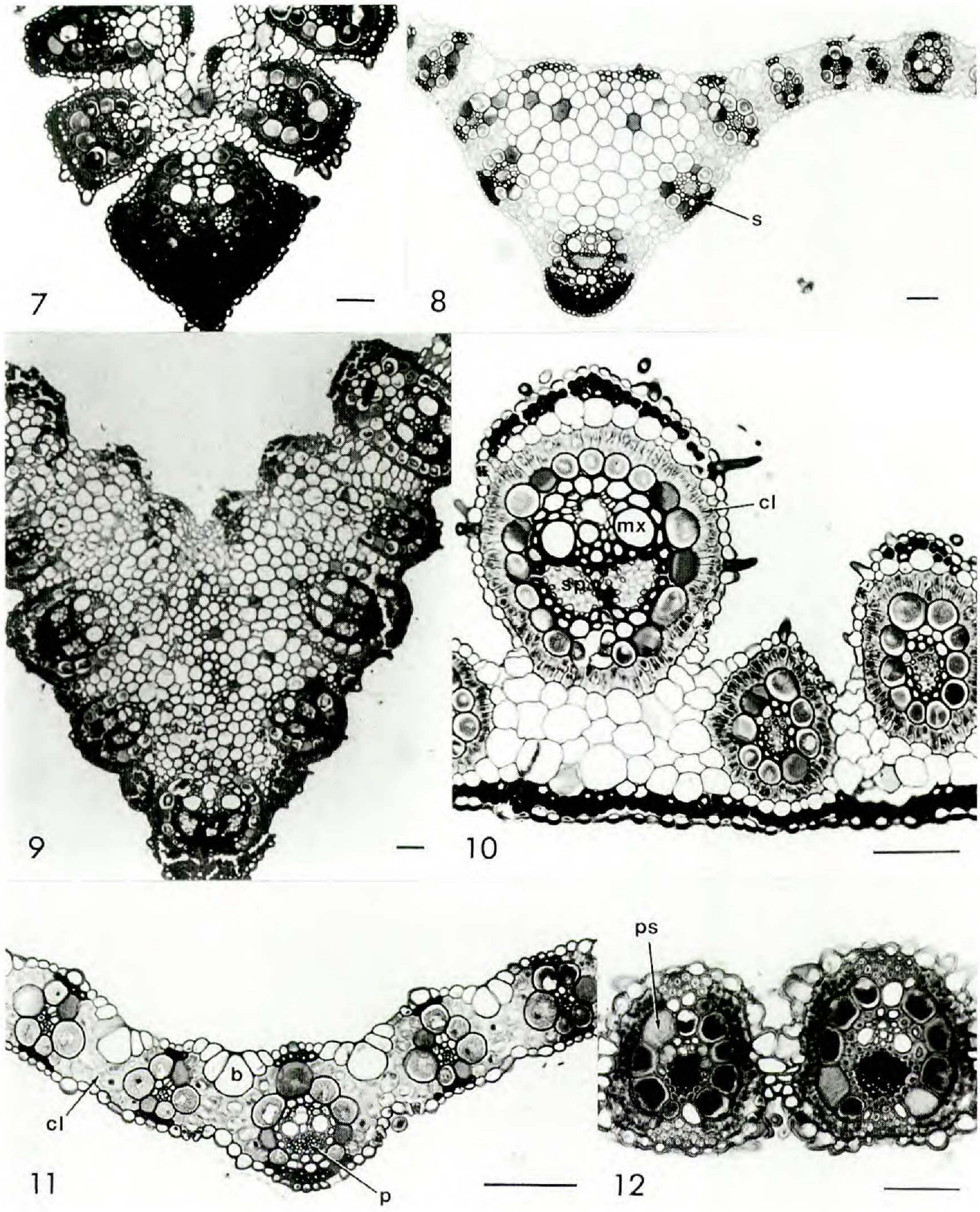
and adaxial fibers, and intercostal sclerenchyma. 3. ***M. dubia*** **with an involute lamina, deep adaxial furrows (1/2 or more than blade thickness), obovate/elliptic vascular bundle shape, adaxial crown of inflated cells, abaxial inflated cells, simple keel with only a single primary vascular bundle, tertiary and secondary vascular bundles <2/3 the size of the primary bundles, with secondary and tertiary vascular bundles positioned closer to the abaxial surface, 15 total vascular bundles per blade, one to three secondary and tertiary vascular bundles between each primary bundle, one or two layers of continuous abaxial sclerenchyma, and a sclerenchyma cap along the blade margins. 4.** ***M. brevivaginata*** **with primary and tertiary vascular bundles about the same size, a simple keel, rounded vascular bundles, an undifferentiated median vascular bundle, centered vascular bundles, and 13 vascular bundles per blade. 5.** ***M. pubigluma*** **with secondary and tertiary vascular bundles that are about 4/5 the width of the primary bundles, two secondary or tertiary vascular bundles between each primary bundle, rectangular vascular bundle shape, centered vascular bundles, tightly radiate chlorenchyma, a column of colorless cells separating each vascular bundle, sclerosed phloem, parenchyma bundle sheath extensions, one or two layers of adaxial sclerenchyma development in the primary bundles, and discontinuous abaxial sclerenchyma development in the primary bundles. 6.** ***M. nigra*** **showing obovate/elliptic vascular bundle shape, tertiary and secondary vascular bundles that are <2/3 the length and width of the primary vascular bundles, tightly radiate chlorenchyma, an adaxial crown of inflated cells, abaxial inflated cells, and secondary and tertiary vascular bundles positioned closer to the abaxial surface. Scale bars = 50 μm; symbols as follows: b = bulliform cell; cl = chlorenchyma, I vb = primary vascular bundle; II vb = secondary vascular bundle; III vb = tertiary vascular bundle; mx = metaxylem; p = phloem; ps = parenchyma bundle sheath; s = sclerenchyma; sp =sclerosed phloem.**

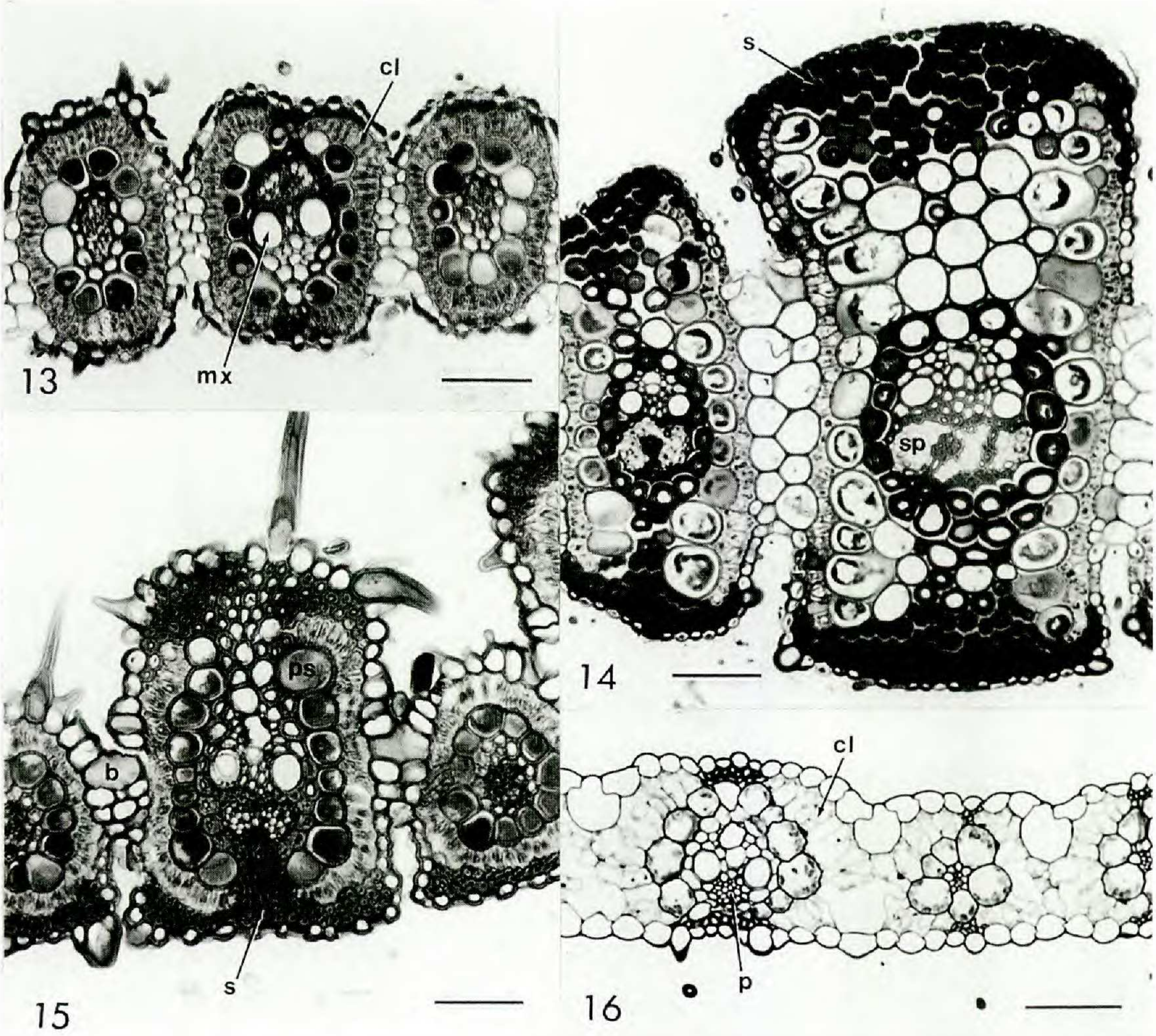


FIGS. 7–12. Leaf blade anatomy of *Muhlenbergia*, adaxial surface uppermost in all photographs. **7.** *M. lehmanniana* with an abaxial projecting midrib of sclerenchyma, with only primary and secondary vascular bundles present, medium vascular bundle differentiated from other primary vascular bundles composed of a complex compound keel with three or more primary and secondary vascular bundles, and abaxial sclerenchyma of two to four discontinuous layers. **8.** *M. japonica* with an abaxial enlarged and bulbous projection of the median vascular bundle, a complex compound keel consisting of a primary vascular bundle and two tertiary vascular bundles with associated parenchyma, with only primary and tertiary vascular bundles, loosely arranged chlorenchyma, and five tertiary vascular bundles between each primary. **9.** *M. gigantea* with a complex compound keel consisting of three or more primary, secondary, and/or tertiary vascular bundles with associated parenchyma, tightly radiate chlorenchyma, and sclerosed phloem. **10.** *M. rigida* showing a primary, tertiary, and secondary vascular bundle (left to right), vascular bundles at three different levels, tightly

The median vascular bundle or midrib is a simple keel (Fig. 4) consisting of a single vascular bundle without associated parenchyma, a compound keel (Fig. 8) consisting of one primary and two secondary or tertiary vascular bundles with associated parenchyma, or a complex compound keel (Fig. 9) consisting of three or more primary, secondary, and/or tertiary vascular bundles with associated parenchyma. All vascular bundles are commonly situated with their position in the median layer of the blade, at the same distance from the adaxial and abaxial leaf surface (Figs. 2, 4, 5, 11, 13), or are occasionally closer to the adaxial surface (Figs. 3, 6, 10) at two or three levels. Vascular bundle composition consists of primary and secondary only in the same blade (Fig. 7), only primary and tertiary in the same blade (Figs. 1, 8, 11). The presence of primary, secondary, and tertiary vascular bundles combined in one blade is not as common (Figs. 3, 6, 10). The total number of primary vascular bundles varies from 5 to 15 (four in *M. fastigiata*, nine in *M. pauciflora*, 15 in *M. gigantea*). Secondary and/or tertiary vascular bundles are arranged in a regular fashion between consecutive primary vascular bundles, and the number varies between 1–3 (Figs. 3, 4, 6), or 4–8 (Fig. 8).

The chlorenchyma tissue consists of two major types (arrangements). It can be composed of a single radiate layer of tightly packed tabular cells that surround each vascular bundle [NAD-ME, centripetally positioned photosynthetic carbon reduction (PCR) cell chloroplasts, XyMS+ and PCR cell outlines that are even in transverse section; see Hattersley and Watson 1992] and is separated by uni-, bi- or tri-serial columns of colorless/bulliform cells (Figs. 3–6, 9, 10, 12–15). Or it can be composed of tabular cells that are indistinctly radiate and continuous between the bundles [PCK type, defined as centrifugal/evenly distributed PCR cell chloroplasts (with grana), XyMS+ and presence of PCR cell wall suberized lamella, in Hattersley and Watson's (1992) sense] (Figs. 1, 11, 16). Colorless cells (Figs. 5, 12, 13) are smaller or similar in size and shape to bulliform cells and are often inflated. A crown of inflated cells is sometimes present over the primary vascular bundles on the adaxial surface and these inflated cells can be found over the secondary vascular bundles as well (Figs. 3, 6, 7, 10, 14). Inflated cells sometimes can be found separating the primary vascular bundles from the epidermis on the abaxial surface (Figs 3, 6, 10). Strips of

radiate chlorenchyma, obovate/elliptic vascular bundle shape, deep adaxial furrows 1/2 or more than the blade thickness, sclerosed phloem, continuous abaxial sclerenchyma, an adaxial crown of inflated cells, abaxial inflated cells, and three or more layers of adaxial sclerenchyma in the primary vascular bundles. 11. ***M. schreberi*** **with 4 – 11 primary vascular bundles between each tertiary vascular bundle, shallow adaxial furrows, centered vascular bundles, loosely arranged chlorenchyma, shield-shaped bulliform cells, and a single layer of adaxial and abaxial (discontinuous) sclerenchyma development in the vascular bundles. 12.** ***M. asperifolia*** **with radiate chlorenchyma, unsclerosed phloem, and a column of colorless cells separting the two vascular bundles. Scale bars = 50 μm; symbols as follows: b = bulliform cell; cl = chlorenchyma, mx = metaxylem; p = phloem; ps = parenchyma bundle sheath; s = sclerenchyma; sp =sclerosed phloem.**



FIGS. 13–16. Leaf blade anatomy of *Muhlenbergia*, adaxial surface uppermost in all photographs. **13.** *M. lindheimeri* with adaxial furrows 1/5 – 1/3 the blade thickness, rectangular vascular bundle shape, centered vascular bundles, non-sclerosed phloem, tightly radiate chlorenchyma, a column of colorless cells separating each vascular bundle, three or more layers of adaxial sclerenchyma, and one or more layers of discontinuous abaxial sclerenchyma. **14.** *M. expansa* with rectangular vascular bundles, sclerosed phloem, tightly radiate chlorenchyma, an adaxial crown of inflated cells in the primary vascular bundle, abaxial and adaxial interrupted parenchyma bundle sheath, abaxial girder of sclerenchyma fibers, circular shaped bulliform cells, three or more layers of adaxial sclerenchyma, and many layers of discontinuous abaxial sclerenchyma. **15.** *M. curvula* with non-sclerosed phloem, tightly radiate chlorenchyma, abaxial and adaxial interrupted parenchyma bundle sheath, abaxial girder of sclerenchyma fibers, three or more layers of adaxial sclerenchyma, many discontinuous layers of abaxial sclerenchyma. **16.** *M. microsperma* shallow adaxial furrows, with loosely arranged chlorenchyma, shield-shaped central bulliform cells, and a few adaxial and abaxial sclerenchyma fibers in the primary bundles. Scale bars = 50 μm; symbols as follows: b = bulliform cell; cl = chlorenchyma, mx = metaxylem; p = phloem; ps = parenchyma bundle sheath; s = sclerenchyma cells; sp =sclerosed phloem.

well-defined and regular bulliform cells are present in the epidermis and are distinct from normal epidermal cells. Bulliform cells can be closely associated with the colorless cells. Bulliform and colorless cells together form the uni-, bi-, or tri-seriate columns which extend from the adaxial furrow to the abaxial epidermis separating the vascular bundles (Figs. 5, 12, 13), or the columns do not extend to the abaxial surface (Fig. 2). The central bulliform cell can be circular to fan-shaped (Fig. 14) or narrower than deep, shield-shaped (Figs. 1, 11, 16). Outer tangential epidermal cell walls are unthickened to slightly thickened, with cells of similar size. Macrohairs have a sunken, nonconstricted base and are embedded between bulliform and/or colorless cells.

The phloem of the primary vascular bundles can be homogeneous or unsclerosed (Figs. 2, 12, 14) or interrupted with sclerenchyma or sclerosed (Figs. 5, 10, 14) where it adjoins the mestome sheath. Two enlarged metaxylem vessels are present adjacent to the phloem and one or two other enlarged protoxylem vessels are located adaxially to the phloem (Figs. 2, 5, 10, 13). Metaxylem vessels are small, not wider than the parenchyma sheath cells, slightly thickened, and circular in outline. A mestome sheath surrounds the xylem and phloem. The mestome cells are small with uniformly thickened walls in all bundles (Figs. 2, 5, 10, 13, 14).

Bundle sheaths in the primary vascular bundles sometimes include extensions (Fig. 5) and are entire (form a complete circle) to adaxially interrupted, or adaxially and abaxially interrupted (Figs. 14, 15) by a broad girder of a few to many sclerenchyma fibers (Figs. 14, 15), or colorless inflated cells (Fig. 14). Secondary and tertiary vascular bundle parenchyma sheaths are mostly entire, not interrupted, to abaxially interrupted in some species. The median vascular bundle parenchyma sheath is mostly abaxially interrupted, to interrupted on both sides, or less frequently not interrupted. Commonly 6–21 cells form the parenchyma sheath of primary vascular bundles (Figs. 2, 5, 10–12, 15, 16), with up to 24 cells found in some species (Fig. 14), while 3–14 cells commonly comprise parenchyma bundle sheaths of secondary (Figs. 5, 10) and tertiary (Figs. 1, 11, 16) vascular bundles.

Adaxial and abaxial sclerenchyma development is extremely variable, from a few fibers (Fig. 1) to 1–3 layers or strands (Figs. 5, 10, 14). In a few species a continuous layer of sclerenchyma can form beneath the epidermis on the adaxial or more commonly abaxial surface (Figs. 3, 4, 6, 10). Sclerenchyma is usually present along the margins of the blades forming a "cap" that may be rounded or pointed (Figs. 3, 4). This sclerenchyma cap adjoins normal mesophyll cells. Sclerenchyma is usually absent between each vascular bundle where there are no continuous sclerenchyma layers. However, a few species, *M. pauciflora* (Fig. 2) and M. *seatonii*, form a conic abaxial girder of intercostal sclerenchyma. An abaxial projection of midrib caused by sclerenchyma is sometimes enlarged and bulbous (Figs. 7, 8).

Cladistics.—For the overall analysis of 148 species (plus two infraspecific taxa) of *Muhlenbergia* and four outgroup species representing four genera (*Eragrostis acutiflora*, *Erioneuron avenaceum*, *Leptochloa virgata*, and

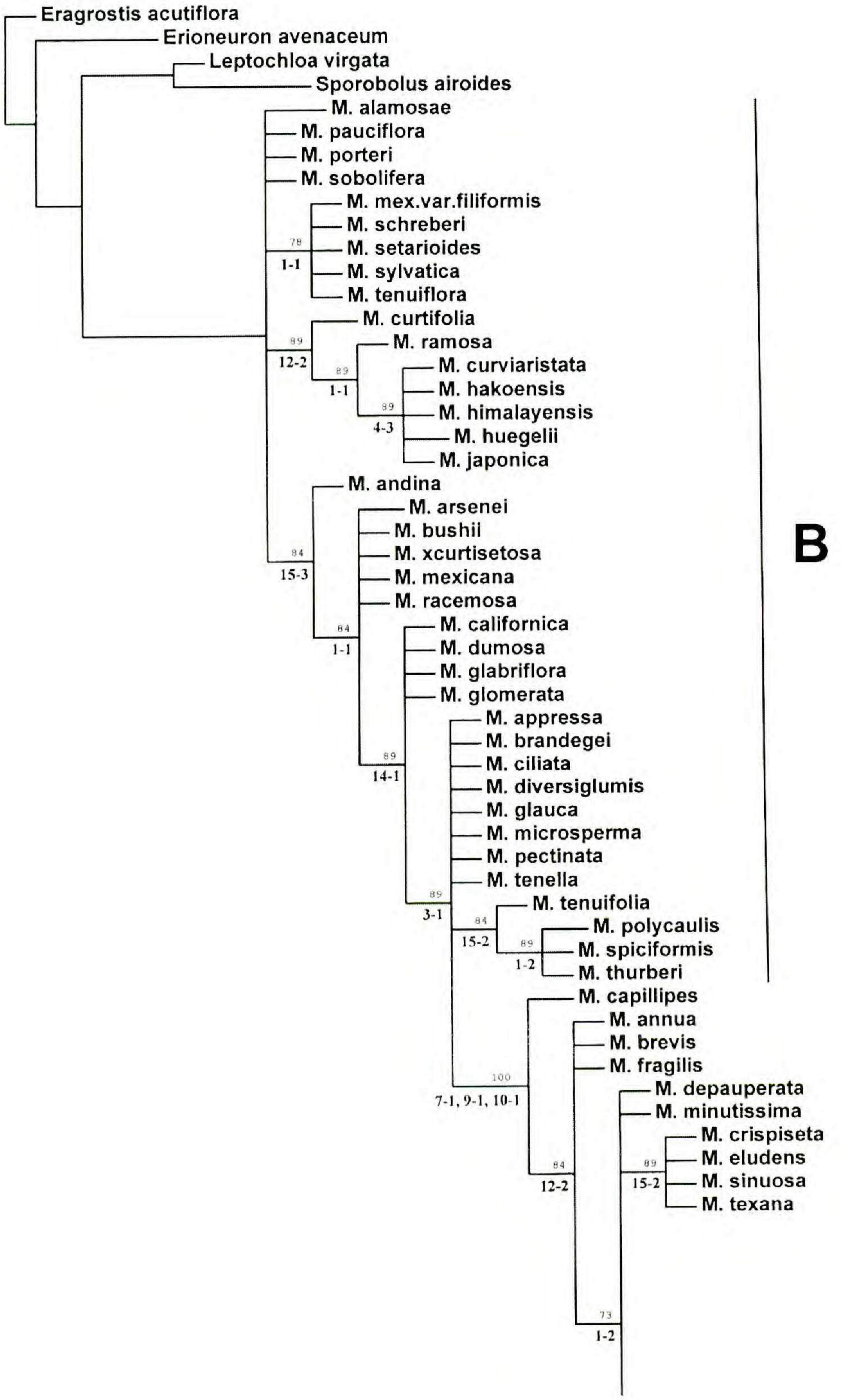
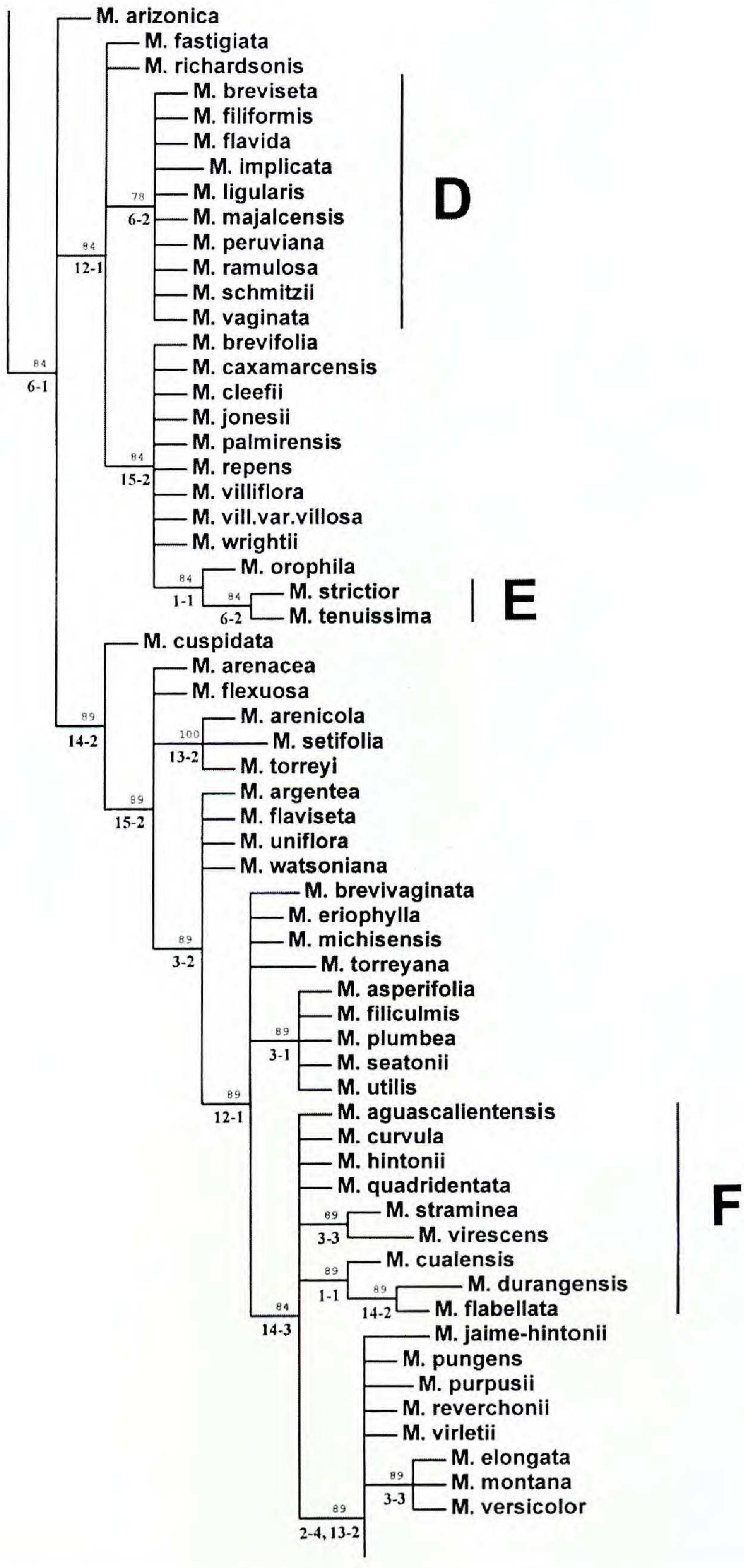


Fig. 17. One of 20 equally parsimonious trees (length = 97 steps, CI = 0.30; RI = 0.89) analyzing 148 species of *Muhlenbergia* with *Eragrostis acutiflora*, *Erioneuron avenaceum*, *Leptochloa virgata*, and *Sporobolus airoides* used as



outgroups. Numbers above a branch are bootstrap values and numbers below indicate the character followed by the state. Groups A-F are discussed in the text.

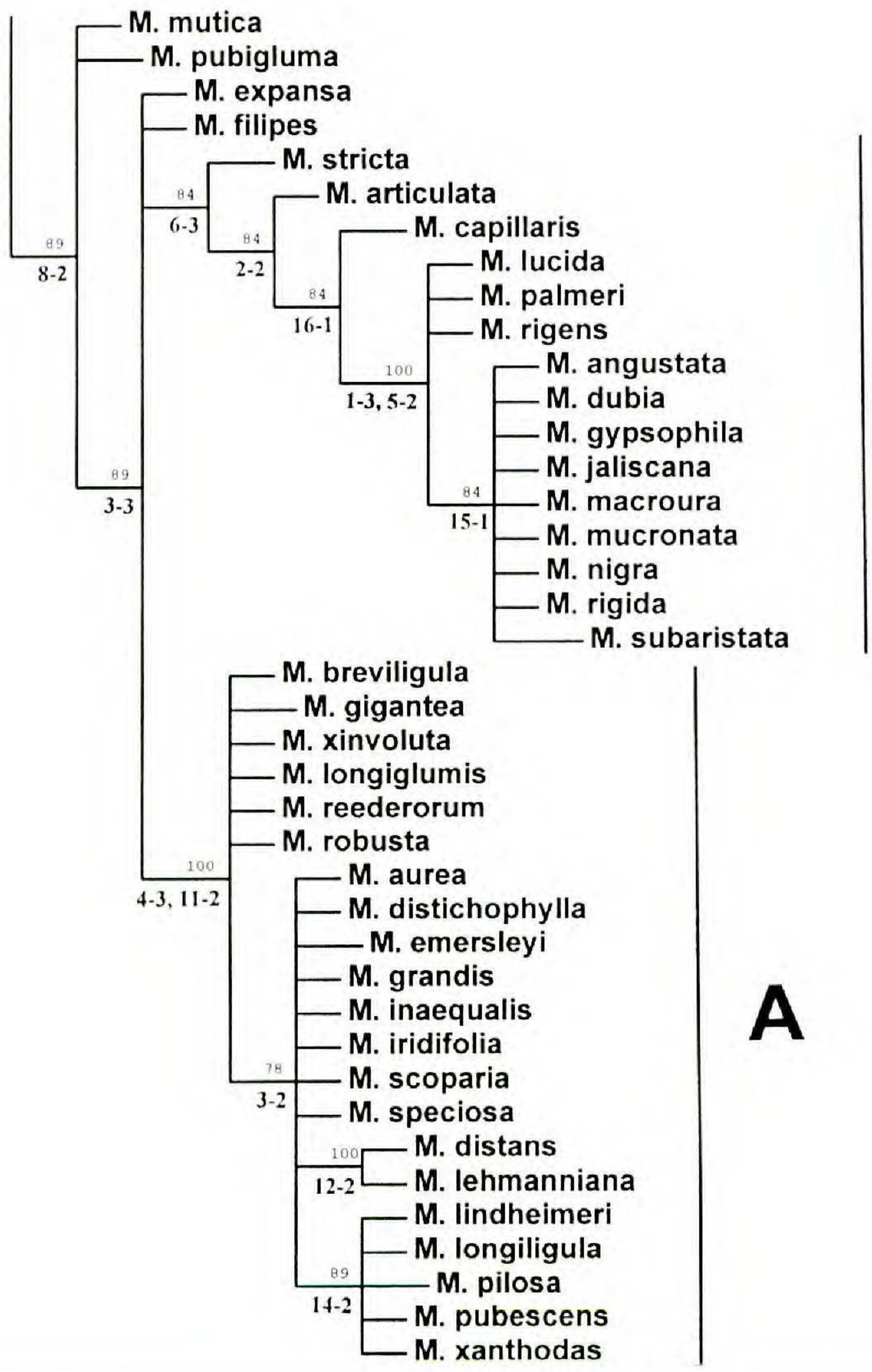


Fig. 17 Continued

Sporobolus airoides) were used simultaneously and in all possible combinations. All possible combinations were obtained by changing the order of each outgroup listed in the data set and sequentially eliminating one, two or three of the outgroups. These 200 trees from the single overall analysis are 97 to 99 steps long, with a consistency index (CI) of 0.30 and a retention index (RI) of 0.89. Twenty of these 200 trees were only 97 steps long and therefore one of these was randomly selected for illustration (Fig. 17). As indicated in the methods, there were no synapomorphies supporting monophyly of the *Muhlenbergia* clade, therefore the outgroup species were constrained. These 16 anatomical characters are not, by themselves robust enough to test for monophyly within the genera of Muhlenbergiinae, Eragrostideae, or the entire Chloridoideae.

There is little resolution in the strict consensus tree for the overall analysis (using the 200 trees). However, the strict consensus tree separates a clade (Fig. 17A) containing *M. aurea*, *M. breviligula*, *M. distans*, *M. distichophylla*, *M. emersleyi*, *M. gigantea*, *M. grandis*, *M. inaequalis*, *M. x involuta*, *M. iridifolia*, *M. lehmanniana*, *M. lindheimeri*, *M. longiglumis*, *M. longiligula*, *M. pilosa*, *M. pubescens*, *M. reederorum*, *M. robusta*, *M. scoparia*, *M. speciosa*, and *M. xanthodas* (bootstrap value of 100%); a clade (when rooted with *Erioneuron avenaceum* in a separate analysis at 0.28 CI and 0.88 RI) or a grade (B), when rooted with *Eragrostis acutiflora* in a separate analysis) containing the following 37 species: *M. alamosae*, *M. andina*, *M. appressa*, *M. arsenei*, *M. brandegei*, *M. bushii*, *M. californica*, *M. ciliata*, *M. curtifolia*, *M. x curtisetosa*, *M. curviaristata*, *M. diversiglumis*, *M. dumosa*, *M. glabriflora*, *M. glauca*, *M. glomerata*, *M. hakoensis*, *M. himalayensis*, *M. huegelii*, *M. japonica*, *M. mexicana* var. *mexicana*, *M. mexicana* var. *filiformis*, *M. microsperma*, *M. pauciflora*, *M. pectinata*, *M. polycaulis*, *M. porteri*, *M. racemosa*, *M. ramosa*, *M. schreberi*, *M. setarioides*, *M. sobolifera*, *M. spiciformis*, *M. sylvatica*, *M. tenella*, *M. tenuiflora*, *M. tenuifolia*, and *M. thurberi* (bootstrap value of 100%); and a grade of all other species in the genus. The former group of 21 species all appear to be members of *M.* subg. *Trichochloa*, sect. *Epicampes* (Soderstrom 1967; Peterson 2000). Two apomorphies support a clade (Fig. 17, clade A): complex compound keels with three or more additional primary, secondary and/or tertiary vascular bundles [character 4(3)] and median vascular bundles that are differentiated from other primary vascular bundles [character 11(2)]. However, complex compound keels [character 4(3)] appear in five additional species in two clades. One of these clades, containing *M. curviaristata*, *M. hakoensis*, *M. himalayensis*, and *M. japonica*, is composed only of species endemic to southeast Asia.

We must point out that *M. mexicana* var. *mexicana* and *M. mexicana* var. *filiformis* occur in two separate clades (Fig. 17, grade A). Both species have identical scores for the data set. However, abaxial sclerenchyma development (character 15) is ambiguously scored as having one or more layers (state 2) or three or more layers (state 3) for each of these taxa. I am not completely familiar with the algorithm used in WinClad2000 but it appears that it selects either state 2 or 3 when reading ambiguous character scores. That would account for the inclusion of *M. mexicana* var. *filiformis* after the node supported by character 15(3), whereas *M. mexicana* var. *mexicana* was selected as 15(2). This is just one of the 20 shortest trees and most of the other trees include both varieties of *M. mexicana* in the same clade.

Three apomorphies of deep adaxial furrows greater than 1/2 the blade thickness [character 1(3)], vascular bundles positioned in two or three levels [character 5(2)], and inflated cells located below (abaxial to) the primary vascular bundles [character 16(1)] support a core group of 12 species (Fig. 17, clade C) that correspond to members of *M.* subg. *Trichochloa*, sect. *Podosemum* (*M.*

angustata, *M. dubia*, *M. gypsophila*, *M. jaliscana*, *M. lucida*, *M. macroura*, *M. mucronata*, *M. nigra*, *M. palmeri*, *M. rigens*, *M. rigida*, and *M. subaristata*). These 12 species plus *M. articulata*, *M. capillaris*, and *M. stricta* form a clade characterized by having vascular bundles composed of primary, secondary, and tertiary types [character 6(3)].

Muhlenbergia capillaris, *M. expansa*, and *M. filipes* are problematic since in other trees these species comprise a single clade or in separate clades. In 70 of the 200 trees these three species form a clade with the 14 previously discussed species tentatively placed in *M.* subg. *Trichlochloa*, sect. *Podosemum*. In all other trees they are aligned with species of *M.* subg. *Trichochloa* in a grade containing clades of each section (*Epicampes* and *Podosemum*). Therefore, placement in either section of *M.* subg. *Trichochloa* is premature. Interestingly, these three species were treated by Morden and Hatch (1989) as a single species with three varieties. Although they can be somewhat difficult to distinguish using gross morphological features, there appears to be sufficient differences in habitat, flowering time, and anatomical structure to warrant recognition at the species level. We believe these three species clearly belong in *M.* subg. *Trichochloa* since they form a clade with other members of sect. *Epicampes* and sect. *Podosemum* by possessing a crown of inflated cells just below (abaxial to) the primary vascular bundles [character 8(2)].

Soderstrom (1967) delineated *M.* subg. *Trichochloa* (as *M.* subg. *Podosemum*) based on possession of sclerosed phloem, caespitose perennial habit with erect, usually stout and robust culms, and glumes veinless or 1-veined. The single apomorphy (symplesiomorphy?) of sclerosed phloem [character 13(2)] appears to be an important character aligning at least 11 additional species in our analysis: *M. elongata*, *M. jaime-hintonii*, *M. montana*, *M. mutica*, *M. pubigluma*, *M. pungens*, *M. purpusii*, *M. reverchonii*, *M. setifolia*, *M. versicolor*, *M. virlettii*. All these species except *M. pungens* have the morphological characteristics that Soderstrom described for *M.* subg. *Trichochloa*. *Muhlenbergia pungens* is rhizomatous, decumbent near the base, and short (culms 20-70 cm tall). Based on our morphological observations *M. pungens* appears related to *M. arenacea*, *M. arenicola*, and *M. torreyi*. The last two species are the only other taxa in our study that have sclerosed phloem [character 13(2)]; however, these two species with *M. setifolia* always form a separate clade. There are no obvious morphological characteristics that align *M. setifolia* with either *M. arenicola* or *M. torreyi*. Therefore, the evolution of sclerosed phloem within *Muhlenbergia* appears to have occurred twice. Even though *M. montana* exhibits some individuals with sclerosed phloem, others lack this character state. *Muhlenbergia montana* was aligned with *M. straminea* and *M. virescens* in about half of the 200 trees and therefore should not be included in *M.* subg. *Trichochloa* at this time. These three densely caespitose species all have 3-veined upper glumes that are usually

3-toothed as well. It seems best to tentatively place these eight species (excluding *M. montana* and *M. pungens*) in *M.* subg. *Trichochloa* without further affinities.

These 200 trees in the overall analysis appear to support a group (Fig. 17, grade B) of 37 species with apomorphies of loosely arranged chlorenchyma [C_4 PCK type; character 7(2)] and fan- to shield-shaped bulliform cells without formation of a sclerenchyma girder from the adaxial to the abaxial surface [character 9(2)]. These 37 species correspond to *M.* subg. *Muhlenbergia*. All of these species except *M. arsenei* and *M. polycaulis* have an additional apomorphy of four or more secondary and/or tertiary vascular bundles between consecutive primary vascular bundle [Character 10(2)]. However, four species (*M. curtifolia*, *M. glauca*, *M. pauciflora*, and *M. thurberi*) exhibit both states for character 10. A homoplasious state in these 37 species is the occurrence of only primary and tertiary vascular bundles [character 6(2)] also shared with annual or short-lived perennial* (Fig. 17, clades D & E) species (*M. annua*, *M. brevis*, *M. breviseta**, *M. capillipes*, *M. crispiseta*, *M. depauperata*, *M. eludens*, *M. filiformis*, *M. flavida*, *M. fragilis*, *M. implicata*, *M. ligularis**, *M. majalcensis*, *M. minutissima*, *M. peruviana*, *M. ramulosa*, *M. schmitzii*, *M. sinuosa*, *M. strictior*, *M. tenuissima*, *M. texana*, *M. vaginata**). However, 120 of the 200 trees suggested direct descent, i.e., derived from a single common ancestor, for the derivation of this state [character 6(2)].

The evolution of C_4 photosynthesis in grasses is a complicated subject, however, it seems clear that the pathway has originated at least four times (Sinha and Kellogg 1996) or more (seven or more times in Brown 1977). One of those origins appears to be the subfamily Chloridoideae lineage (Renvoize and Clayton 1992). Our study suggests that in *Muhlenbergia* the PCK subtype of photosynthesis was a single evolutionary event [character 7(2)]. Since the occurrence of the PCK subtype is found in three of the four outgroup species (*Eragrostis acutiflora*, *Leptochloa virgata*, and *Sporobolus airoides*), it is not surprising that in all 200 trees this state appears plesiomorphic when rooted with these species. Hattersley and Watson (1992) hypothesized that the PCK subtype evolved from NAD-ME since in the C_4 acid cycle PCK subtype is an enhancement of the NAD-ME subtype, and PCK is only known in grasses and may therefore have evolved subsequent to the NAD-ME type which is known in other monocotyledons and dicotyledons. Jacobs (1987) earlier suggested that the PCK subtype is perhaps primitive since it is found in other groups, i.e., Panicoideae, whereas the NAD-ME subtype is restricted to Chloridoideae. We agree with Hattersley and Watson's assessment and prefer to view the development of the PCK subtype in *Muhlenbergia* as the derived state. An alternative hypothesis, although this would require additional morphological or molecular evidence, might be that the PCK species or *M.* subg. *Muhlenbergia* actually represent a separate lineage and deserves generic status.

The remaining 64 taxa (*M. aguascalientensis*, *M. annua*, *M. arenacea*, *M. arenicola*, *M. argentea*, *M. arizonica*, *M. asperifolia*, *M. brevifolia*, *M. brevis*, *M. breviseta*, *M. capillipes*, *M. caxamarcensis*, *M. cleefii*, *M. crispiseta*, *M. cualensis*, *M. curvula*, *M. cuspidata*, *M. depauperata*, *M. durangensis*, *M. eludens*, *M. eriophylla*, *M. fastigiata*, *M. filiculmis*, *M. filiformis*, *M. flabellata*, *M. flavida*, *M. flaviseta*, *M. flexuosa*, *M. fragilis*, *M. hintonii*, *M. implicata*, *M. jonesii*, *M. ligularis*, *M. majalcensis*, *M. michisensis*, *M. minutissima*, *M. montana*, *M. orophila*, *M. palmirensis*, *M. peruviana*, *M. plumbea*, *M. pungens*, *M. purpusii*, *M. quadridentata*, *M. ramulosa*, *M. repens*, *M. richardsonis*, *M. schmitzii*, *M. seatonii*, *M. sinuosa*, *M. sinuosa*, *M. straminea*, *M. strictior*, *M. tenuissima*, *M. texana*, *M. torreyana*, *M. torreyi*, *M. utilis*, *M. vaginata*, *M. villiflora* var. *villiflora*, *M. villiflora* var. *villosa*, *M. virescens*, *M. watsoniana*, and *M. wrightii*) seem to contain sympleisiomorphies, i.e., they lack anatomical synapomorphies. These species all exhibit radiate, compact chlorenchyma or the classical NAD-ME subtype characteristic of many chloridoid grasses [character 7(1)]; contain primary vascular bundles without sclerosed phloem [character 13(2)], although present in *M. arenicola*, *M. pungens*, and *M. torreyi*; have rounded vascular bundles [character 2(1)], although *M. torreyana* and *M. pungens* have obovate/elliptic or rectangular bundles; have simple keels [character 4(1)], although *M. torreyana* has a complex compound keel like species in *M.* subg. *Trichochloa* sect. *Epicampes*; and have circular or irregular to fan-shaped bulliform cells [character 9(1)]. Even though the cladistic analysis using these 16 anatomical characters does not suggest a monophyletic lineage for these 63 species, we prefer to recognize them informally as the 'Clomena' complex (Peterson 2000).

Within 'Clomena' there exists some resolution, for instance, a clade containing annual or short-lived perennial species (Fig. 17, clade D) is based on the occurrence of primary and secondary vascular bundles [character 6(2)]. Other annuals (*M. annua*, *M. brevis*, *M. crispiseta*, *M. depauperata*, *M. eludens*, *M. fragilis*, *M. minutissima*, *M. sinuosa*, and *M. texana*) occur as a grade. A grade (Fig. 17, grade F) within 'Clomena' containing *M. aguascalientensis*, *M. cualensis*, *M. curvula*, *M. durangensis*, *M. flabellata*, *M. hintonii*, *M. quadridentata*, *M. straminea*, and *M. virescens*, along with the remaining species in the analysis is also depicted. These species along with *M. argentea*, *M. crispiseta*, *M. eriophylla*, *M. filiculmis*, *M. flaviseta*, *M. jonesii*, *M. michisensis*, *M. montana*, *M. peruviana*, and *M. watsoniana* have been referred to as the *Muhlenbergia montana* complex (Herrera-Arrieta 1998; Herrera-Arrieta and De la Cerda-Lemus 1995; Herrera-Arrieta and Grant 1993,1994). This complex consists of highly caespitose species usually with a three-veined upper glumes, and in our analysis, leaf blades mostly with three or more layers of adaxial sclerenchyma in the primary bundles [character 14(3)]. The *Muhlenbergia repens* complex (Morden 1985, 1995; Morden and Hatch 1987, 1996) which includes *M. fastigiata*, *M. plumbea*, *M. repens*, *M. richardsonis*, *M. utilis* and *M. villiflora*) is not monophyletic, i.e., these species are found in two or more clades or as a grade with many additional species.

One of the two least homoplasious characters in the analysis is chlorenchyma arrangement (character 7, consistency index = 0.50). All species in *M.* subg. *Muhlenbergia* appear to be PCK [character 7(2)] whereas all other members of the genus are NAD-ME [7(1)]. Only two species are ambiguously scored for character seven, *M. glauca*, more than likely a member of *M.* subg. *Muhlenbergia*, and *M. capillaris*, clearly a member of *M.* subg. *Trichochloa*. Median vascular bundle structure (character 11, CI = 0.50) is the other least homoplasious character. All members of *M.* subg. *Trichochloa* sect. *Epicampes* have median vascular bundles that are differentiated from other primary vascular bundles [11(2)]. If you choose to disregard the outgroup species in the cladistic analysis, then within *Muhlenbergia* there is no homoplasy (CI = 1.00) for these two characters (7 & 11).

In conclusion, our data support the division of *Muhlenbergia* into two subgenera (*M.* subg. *Muhlenbergia* and *Trichochloa*) and two sections (*M.* sect. *Epicampes* and *Podosemum*) in *M.* subg. *Trichochloa*. Preliminary investigations of *Muhlenbergia* and relatives based on internal transcribed spacer region sequences of nuclear ribosomal DNA provide support for a clade containing only PCK species (= *M.* subg. *Muhlenbergia*) and another clade containing only *M.* subg. *Trichochloa* (Peterson, Columbus, Cerro Tlatilpa, and Kinney 2001). We prefer to view this partial classification based on anatomical characters as a work in progress and realize that with additional morphological and molecular data our understanding of the evolution of this genus will improve. We feel it is important to present this anatomical information since it is the first time the entire genus has been surveyed in this manner, therefore this serves as a foundation for further taxonomic research.

APPENDIX 1

Specimens used in this study, all housed at the United States National Herbarium (US) unless otherwise indicated. Those marked with an asterisk * appear in the figures. Collectors are abbreviated as follows: **A** = C.R. Annable; **AC** = S. Acevado; **B** = S.M. Braxton; **C** = A. Cortes O.; **CA** = M.A. Carranza; **CV** = A. Campos-Villanueva; **D** = C.H. Dietrich; **DC** = M. De la Cerda-Lemus; **DU** = W.C. Dunn; **G** = M.S. Gonzalez-Elizondo; **H** = Y. Herrera-Arrieta; **J** = E.J. Judziewicz; **K** = M.B. Knowles; **KI** = R.M. King; **L** = J. Linkins; **LB** = R.J. LeBlond; **M** = O. Morrone; **P** = P.M. Peterson; **PO** = M.E. Poston; **R** = N. Refulio-Rodriguez; **S** = R.J. Soreng; **V** = J. Valdes-Reyna; **VI** = J.A. Villarreal; **W** = A.S. Weakley.

TAXON	COLLECTORS	LOCALITY
M. aguascalientensis Y. Herrera & de la Cerda-Lemus	H&DC 1185	MEXICO. Aguascalientes: San Jose de Gracia, 12 km NW of La Congoja
M. alamosae Vasey	P&A 8293	MEXICO. Chihuahua: 76 mi W La Junta and 35.2 mi W Tomochic in Parque Nal. Cascada de Basaseachic
	P,A&V 10807	MEXICO. Chihuahua: Parque Natural Barranca del Cobre, 12.6 mi NE La Bufa and 2 mi S Basigochi
M. andina (Nutt.) Hitchc.	P&A 4982	USA. California: San Benito Co. 9.8 mi SW New Idria along Clear Creek
M. angustata (J. Presl) Kunth	P,A&PO 8817	ECUADOR. Provincia de Chimborazo: 8.9 km N Palmira on the Panamerican Hwy
M. annua (Vasey) Swallen	P&A 4036, 4053	MEXICO. Chihuahua: NW of Hernandez Javales
	P&A 4102	MEXICO. Durango: Navios
M. appressa C.O. Goodd.	P&A 4189	USA. Arizona: Graham Co. 6.6 mi SW Hwy 366 above jtn. with Hwy 666
	Holmgren & Holmgren 7051	(NY)USA. Arizona: Graham Co., Pinaleno Mts.
M. arenacea (Buckley) Hitchc.	P&A 5703	USA. Arizona: Cochise Co., Triangle T Road, 1.2 mi E Dragoon
	P,A&V 10033	MEXICO. Coahuila: 29.2 mi S Saltillo on Mex 54 to Concepcion del Oro
M. arenicola Buckley	P&A 5521	USA. Arizona: Cochise Co., 10 mi S Rucker Canyon on Tex Canyon Road & 6 mi NE Hwy 80.
	P,A&V 10032	MEXICO. Coahuila: 29.2 mi S Saltillo on Mex 54 to Concepcion del Oro
M. argentea Vasey	P,A&H 8044	MEXICO. Chihuahua: 15.3 mi S Mex 127 and 6.9 mi NE La Bufa
M. arizonica Scribn.	P&A 5329	USA. Arizona: Santa Cruz Co. 3.3. mi W Hwy 289 & Pena Blanca
M. arsenei Hitchc.	P&A 5142	MEXICO. Baja California: Sierra San Pedro Martir, 1.8 mi S Vallecitos
M. articulata Scribn.	P&K 13386	MEXICO. San Luis Potosi: 2.5 mi E Hwy 57 on road towards Guadalcazar
	P&K 13365	MEXICO. Nuevo Leon: ca 36 mi N Dr. arroyo on Hwy 61 towards Linares
M. asperifolia (Nees & Meyen ex Trin.) Parodi	P&A 4851	USA. Oregon: Klamath Co. 1.5 mi S Worden on Hwy 97
	P,A&M 10177*	ARGENTINA. Provincia Salta: at km 1137, 26.7 km SE Molinos on Hwy 40
M. aurea Swallen	M de Koninck 1954	GUATEMALA. Quetzaltenango: Retalhuleu

TAXON	COLLECTORS	LOCALITY
M. brandegei C. Reeder	Moran 9361	MEXICO. Baja California Sur: Isla Catalina
	P&A 4760	MEXICO. Baja California Sur: Isla La Partida
M. brevifolia Scribn. ex Beal	P,A&V 10811	MEXICO. Chihuahua: 12.6 mi NE of La Bufa and 2 mi S of Basigochi
M. breviligula Hitchc.	A.S. Hitchcock 9063	GUATEMALA. Guatemala city
M. brevis C.O. Goodd.	P&A 4005	USA. New Mexico: Grant Co., NE of San Lorenzo
	P&A 4030	MEXICO. Chihuahua: NW of Hernandez Javales
M. breviseta Griseb. ex E. Fourn.	A.S. Muller 1853	MEXICO. Veracruz: Orizaba
M. brevivaginata Swallen	P,D,B&K 13396	MEXICO. Sinaloa: 3 mi SW Estado de Durango and 2.2 mi S El Palmito on Hwy 40
	P,G&K 13660*	MEXICO. Durango: 7.3 mi S of Charcos on road towards San Juan de Michis
M. bushii R.W. Pohl	D.M. Moore 30573	USA. Arkansas: Benton Co., Monte Ne
M. californica Vasey	P&A 5013	USA. California: San Bernardino Co., Mtn. Home Village, along Mtn. Home Creek
M. capillaris (Lam.) Trin.	P,W&LB 14236	USA. North Carolina: Brunswick Co., Sunset Beach
M. capillipes (M.E. Jones) P.M. Peterson & Annable	P&A 5858	MEXICO. Chihuahua: 24 mi SW La Junta and approx. 44 mi N Creel, at P Arroyo Ancho crossing
	P 9604 MEXICO.	Chihuahua: 23 mi SW La Junta on road to Creel at the Puente Arroyo Ancho
M. caxamarcensis Laegaard &	P&R 14013	PERU. Depto. Cajamarca: Prov. Cajamarca, 18 km W of Central Plaza of Cajamarca up road to Cumbemayo Sanchez Vega
M. ciliata (Kunth) Trin.	P&A 4679*	MEXICO. Chiapas: 8.2 mi SE of San Cristobal de las Casas
M. cleefii Laegaard	Cleef & Florschutz 5578	COLOMBIA. Boyaca: Sierra Nevada del Cocuy, Alto Valle Lagunillas
M. crispiseta Hitchc.	P&A 4063	MEXICO. Chihuahua: 12.1 mi NE of El Vergel on Hwy 24
	P&A 4067	MEXICO. Chihuahua: 10.9 mi NE of El Vergel on Hwy 24
	P&A 4103	MEXICO. Durango: 5.4 mi W of Navios, 42 mi W of Durango
M. cualensis Y. Herrer & P.M. Peterson	Guzman 6090	MEXICO. Jalisco: E of Zimapan mine
M. curtifolia Scribn.	P&A 5631	USA. Arizona: Cocoino Co., Oak Canyon 22.5 mi SE of Fredonia on Forest Service Road 422
M. xcurtisetosa (Scribn.) Bush	G.P. Clinton 1892	USA. Illinois: Champaign
M. curviaristata (Ohwi) Ohwi	T. Koyama 6390	JAPAN. Honshu: Prov. Shinano, Togakushi, 2 km NW of Chusha
M. curvula Swallen	P,G&K 13636	MEXICO. Durango: 30 mi SE Mezquital on road to Charcos
	P 9686*	MEXICO. Guanajuato: 18.5 mi SE San Felipe on Mex 37 to Leon

TAXON	COLLECTORS	LOCALITY
	P,A&V 10056	MEXICO. Coahuila: 32 mi SE Saltillo and 8 mi SE JAme on road to Sierra La Viga
	P,A&V 10057	MEXICO. Coahuila: 32 mi SE Saltillo and 8 mi SE JAme on road to Sierra La Viga
M. cuspidata (Torr.) Rydb.	P&A 5544	USA. New Mexico: Grant Co., 8 mi E Central on Hwy 90
M. depauperata Scribn.	P&A 4082	MEXICO. Chihuahua: Just N of Villa Matamoros on Hwy 45
	P&A 4088	MEXICO. Durango: 64 km N of Durango on Hwy 45
	P&A 4091	MEXICO. Durango: 20 km S of Durango on road towards Aserradero La Flor
M. distans Swallen	P&A 5886	MEXICO. Chihuahua: 5.3 mi S of Cusarare on road to Guachochi
	P&A 6010	MEXICO. Durango: 40 km W of Durango on Hwy 40, 6 mi W of Rio Chico
M. distichophylla (J.Presl) Kunth	P,D,B&K 13583	MEXICO. Chihuahua: Parque Natural Barranca del Cobre, 1 mi E of La Bufa
M. diversiglumis Trin.	P&A 4132	MEXICO. Durango: 18.6 mi W of El Salto, 81.2 mi W Dgo.
	P&A 4137	MEXICO. Durango: 22.7 mi W of La Ciudad on Hwy 40
	P&A 4147	MEXICO. Sinaloa: 2 mi E of Sta. Rita
	P&A 4163	MEXICO. Sinaloa: 1.1 mi NW of Mocorito
M. dubia E. Fourn.	P&A 5550	USA. New Mexico: Grant Co., 12 mi E Central on Hwy 90
	P&A 5558	USA. New Mexico: Grant Co., 0.7 mi NW junction Hwy 61 & 35, on Hwy 35
	P&A 5809	MEXICO. Chihuahua: Colonia Cumbres de Majalca, approx. 20 mi W Hwy 45, N of Chihuahua
	P,A&H 8028	MEXICO. Chihuahua: 25.6 mi S Creel on road to Batopilas
	P,V,VI 8391	MEXICO. Coahuila: SE San Antonio de las Alazanas & SE of Saltillo, at end of road near summit of Coah.
	P&A 10593	MEXICO. Coahuila: 87 mi NW Muzquiz on Hwy 53 towards Boquilla del Carmen
	P&A 10594*	MEXICO. Coahuila: 87 mi NW Muzquiz on Hwy 53 towards Boquilla del Carmen
	P&K 13328, 13330	MEXICO. Nuevo Leon: 6.7 mi W 18 de Marzo, up road towards Cerro del Potosi
M. dumosa Scribn. ex Vasey	P&A 5942	MEXICO. Chihuahua: 12 mi SE Balleza towards Parral
M. durangensis Y. Herrera	P,G&K 13644	MEXICO. Durango: 6 mi S Charcos on road towards San Juan de Michis
	H&AC 981 (CIIDIR)	MEXICO. Durango: Ca. 10 km W of San Juan de Michis
M. elongata Scribn. ex Beal	P&A 5680	USA. Arizona: Pima Co., Santa Rita Mts. Box Canyon, 7 mi W Hwy 83 on Forest Service Road 62
M. eludens C. Reeder	P&A 4014	USA. Arizona: Cochise Co., along Rucker Creek

TAXON	COLLECTORS	LOCALITY
	P&A 4096	MEXICO. Durango: 2.1 mi W of Rio Chico crosing, 21 mi W Dgo.
	P&A 4106	MEXICO. Durango: 5.4 mi W of Navios, 42 mi W of Durango
	P&A 4516	MEXICO. Chihuahua: 9.1 mi E of Cumbres de Majalca
M. emersleyi Vasey	P&A 5068	MEXICO. Baja California: Sierra San Pedro Martir, 0.6 mi E the W Park entrance
	P&A 5326	USA. Arizona: Santa Cruz Co. 3.3 mi W Hwy 289 & Pena Blanca
	P&A 7917	USA. New Mexico: Grant Co., Line along Hwy 78, 6 mi W of Mule Creek
	P&A 7918	USA. New Mexico: Grant Co., Line along Hwy 78, 6 mi W of Mule Creek
	P,A&H 8018	MEXICO. Chihuahua: 24.3 mi S Creel on road to Batopilas, at the Barranca El Cobre
	P,A&V 10765	MEXICO. Chihuahua: 35 mi W Balleza and 24 mi E Guachochi
	P,A&V 10805	MEXICO. Chihuahua: Parque Natural Barranca del Cobre, 12.6 mi NE La Bufa and 2 mi S Basigochi
M. eriophylla Swallen	G 1626 (CIIDIR)	MEXICO. Durango: Arroyo El Temazcal, 4 km al SW de Piedra Herrada
	H&C 930 (CIIDIR)	MEXICO. Michoacan: Cerro Ucarero, Zinapecuaro, 2 km al S de Querendaro
M. expansa (Poir.) Trin.	Boyce & Godfrey 1581	USA. North Carolina: Cumberland Co., 13 mi N of Fayetteville on route 15
	P,W&LB 14234*	USA. North Carolina: Columbus Co., Old Dock Savanna.
M. fastigiata (J. Presl) Henrard	P,A&M 10286	ARGENTINA. Provincia Jujuy: 4 km E of Tres Cruces on road to Humahuaca
	P,A&M 10321	ARGENTINA. Jujuy: 24 km W La Quiaca on Hwy 5 towards Sta Cabalina
M. filiculmis Vasey	P&A 5627	USA. Arizona: Coconino Co., Kaibab Plateau, 4 mi N Kaibab Lodge, Pleasant Valley, along Hwy 67
	P&A 7860	USA. Colorado: Saguache Co., NW of Saguache, 14 mi up Cochetopa pass road (F5750) from Hwy 114
	P&A 3994	USA. Arizona: Apache Co., E of McNary
	P&A 2648	USA. California: Tulare Co., Lion Meadow
M. filiformis (Thurb. ex S. Watson) Rydb.	P&A 3987	USA. Washington: Klickitat Co., Washington State Fish Hatchery
	P&A 3994	USA. Arizona: Apache Co., 7.4 mi E of McNary off Hwy 260
	P&A 4511	USA. Colorado: Pitkin Co., 13 mi S of Leadville on Hwy 24
M. filipes M.A. Curtis	E.P. Killip 42315	USA. Florida: Monroe Co., Big Pine Key
M. flabellata Mez	Pittier 3372	COSTA RICA. San Jose: Cerro Buena Vista
	Pohl & Davidse 11621	COSTA RICA. San Jose: Cerro Buena Vista

TAXON	COLLECTORS	LOCALITY
M. flavida Vasey	P&A 4138	MEXICO. Durango: 22.7 mi W of La Ciudad on Hwy 40
	P&A 4153	MEXICO. Sinaloa: 48.6 mi NE of Mococrito, 8.5 mi S of Surutato
	P&A 4162	MEXICO. Sinaloa: 1.1 mi NW of Surutato, 61.1 mi NE of Mocorito
M. flaviseta Scribn.	P&A 5911	MEXICO. Chihuahua: S side of Barranca El Cobre, approx. 20 mi S Cusarare on road to Guachochi
	H 993 (CIIDIR)	MEXICO. Durango: Parque El Tecuan, 58 km ESE of Durango on Hwy 40 to Mazatlan
	H&AC 982 (CIIDIR)	MEXICO. Durango: 4.5 km SW of San Juan de Michis on road to Piedra Herrada
M. flexuosa Hitchc.	J.F. Macbride s.n.	PERU. Huacachi: Estacion near Muna
M. fragilis Swallen	P&A 4017	USA. Arizona: Santa Cruz Co., SW of Camelo
	P&A 4024	USA. Arizona: Santa Cruz Co., Sycamore Canyon
	P&A 4554	MEXICO. Chihuahua: 13.5 mi W of Parral on Hwy 24
	P&A 4150	MEXICO. Sinaloa: 34.5 mi NE of Mocorito, 22.6 mi S of Surutato
M. gigantea (E. Fourn.) Hitchc.	P 13786	MEXICO. Nayarit: 8 mi E of Compostela on roads towards Chapalilla and Guadalajara
	P,D,B&K 13414*	MEXICO. Sinaloa: 3 mi SW Estado de Durango and 2.2 mi S El Palmito on Hwy 40
M. glabriflora Scribn.	R.M. Kriebel 5802	USA. Indiana: Daviess Co., 6 mi N of Washington
M. glauca (Nees) B.D. Jacks.	P&KI 8237	MEXICO. Chihuahua: 76 mi W La Junta and 35.2 mi W Tomochic in Parque Nacional Cascad Basaseachic
	P,A&V 10072	MEXICO. Coahuila: 17 mi SE Saltillo and 7.4 mi NW Jame at Bosque de Montana
	P&A 5511	USA. Arizona: Cochise Co., Chiricahua Mts., Red Rock Canyon, aprox. 2 mi Rucker Canyon Road
	P&A 5482	USA. Arizona: Cochise Co., 2.4 mi above Upper Picnic Area, Fort Huachuca Military Reservation
M. glomerata (Willd.) Trin.	P&A 5562	USA. New Mexico Catron Co., Canyon leading to Cliff Dwellings and upper end of Hwy 15
M. grandis Vasey	P,D,B&K 13413	MEXICO. Sinaloa: 3 mi SW Estado de Durango and 2.2 mi S El Palmito on Hwy 40
M. gypsophila Reeder & C. Reeder	P&K 13289	MEXICO. Nuevo Leon: 5.6 mi E junction Hwy 57 on Hwy 58 towards Linares
	P&K 13299	MEXICO. Nuevo Leon: 13.4 mi E Hwy 57 on Hwy 58 at crossin Rio Potosi

TAXON	COLLECTORS	LOCALITY
M. hakonensis (Hack. ex Matsum.) Makino	T. Tateoka s.n.	JAPAN. Hakone: Kanagwa-ken
M. himalayensis Hack. ex Hook.	S&P 5666	CHINA. Xizhang (Tibet) Prov.: Markam Co. Ningjing Shan, Markham Range between Mekong & Yantze
M. huegelii Trin.	S&P 5324	CHINA. Sichuan Prov.: Wenchuan Co. W side of front range NW of Sichuan Basin
	S&P 5344	CHINA. Sichuan: Qiunglai Slan, ca 40 km W Wezlou and ca. 120 km NW Clongdu
M. hintonii Swallen	G.B. Hinton 3059	MEXICO. Mexico: crucero Temazcaltepec
M. implicata (Kunth) Trin.	P&A 4514	MEXICO. Chihuahua: 0.7 mi W of Nuevo Majalca, 8.5 mi W of Hwy 45
	P&A 4090	MEXICO. Durango: 20 km S of Durango on road towards La Flor
	P&A 4095	MEXICO. Durango: 2.1 mi W of Rio Chico crossing, 21 mi W of Durango on Hwy 40
M. inaequalis Soderstr.	A.S. Muller 953	VENEZUELA. Trujillo: Quebrada de Duri
M. xinvoluta Swallen	P&A 6267	MEXICO. Nuevo Leon: 10 mi E of Los Lirios and 12 mi W of Laguna de Sanchez
	P&A 6281	USA. Texas: Blanco Co., 0.3 mi E Hwy 280 on Tex 473
M. iridifolia Soderstr.	P&A 6133, 6135	MEXICO. Jalisco: 50 mi W of Ameca on road to Mascota
M. jaime-hintonii P.M. Peterson & Valdes-Reyna	V&C 2560	MEXICO. Nuevo Leon: La Joya, Cuesta Blanca, 15 km S of Aramberri
M. jaliscana Swallen	P&A 6137	MEXICO. Jalisco: 50 mi W of Ameca on road to Mascota
	P&A 6149	MEXICO. Jalisco: Pass above Talpa de Allende, 3.6 mi W of Rio Mascota
M. japonica Steud.	S&P 5240	CHINA. Yunnan Prov.: Fugong (N 1/2 Bijiang) Co. W slopes of Bilou Mts.
	S&P 5301*	CHINA. Kiangwang Shan: ca 15 km E of Dongchuan, ca 120 km NNE of Kunming
M. jonesii (Vasey) Htichc.	P&A 4857	USA. California: Siskiyou Co. Shasta-Trinity National Forest, 9.5 mi SE Hwy 97, on military pass road
M. lehmaniana Henrard	P&A 7372*	PANAMA. Province of Chiriqui: between Rio Quebrado
M. ligularis (Hack.)Hitchc.	P,A&PO 8884	ECUADOR. Provincia de Azuay: 5.6 km S LA Paz on the Panamerican Hwy, and 36.3 km N Ona
M. lindheimeri Hitchc.	P,A&V 10068*	MEXICO. Coahuila: 26.7 mi Se Saltillo and 2.7 mi SE Jame on road to Sierra La Viga
M. longiglumis Vasey	P 13710	MEXICO. Jalisco: 8.2 mi NW Cuautla on road towards Los Volcanes
M. longiligula Hitchc.	P&A 5408	USA. Arizona: Santa Cruz Co. Patagonia Mts., along road to Red Mt., 7.6 mi SE of Patagonia

TAXON	COLLECTORS	LOCALITY
	P&A 7919	USA. New Mexico: Grant Co., Line along Hwy 78, 6 mi W of Mule Creek
	P&KI 8207	MEXICO. Chihuahua: 33.7 mi W La Junta on road to Parque Nacional Cascada de Basaseachic
	P 9605	MEXICO. Chihuahua: 20.8 mi SW La Junta on road to Creel
M. lucida Swallen	P&A 5882	MEXICO. Chihuahua: 5.3 mi S Cusarare on road to Guachochi
	P,A&H 8039	MEXICO. Chihuahua: 10.7 mi S Mex 127 on road to Batopilas
M. macroura (Kunth) Hitchc.	P&CA 9769	MEXICO. Oaxaca: 11.4 mi W San Juan Mixtepec and 1.5 mi E San Isidro Chicahuaxtla
	P,A&V 10986	MEXICO. Michoacan: 8.4 mi SE Zacapu on Mex 15 towards Quiroga
M. majalcensis P.M. Peterson	P&A 4573	MEXICO. Chihuahua: E of Cumbres de Majalca
M. mexicana (L.) Trin.	P&A 4765	USA. Idaho: Lemhi Co., 2.5 mi E of Salmon River on Warm Springs Creek
M. mexicana var. *filiformis* (Torr.) Scribn.	Morton 11689	CANADA. Ontario: Lake Timiskaming (Dawson Point)
M. michisensis Y. Herrera & P.M. Peterson	H&A 986 (CIIDIR)	MEXICO. Durango: San Juan de Michis, Potrero Las Escobas
M. microsperama (DC.) Trin.	P,A&PO 8913	ECUADOR. Provincia de Azuay: 10.2 km N Ona on the Panamerican Hwy
	P,J&KI 9060	ECUADOR. Provincia de Pichincha: 13 km N Calderon on the Panamerican Hwy
	P&A 4759	MEXICO. Baja California Sur: 25 km S of La Paz, W side of Isla La Partida
	P&A 4169	MEXICO. Sonora: 18.2 mi E of Los Tanques on road to Milpillas
	P&A 4023	USA. Arizona: Santa Cruz Co., Sycamore Canyon
	P,A&DU 3067*	USA. Nevada: Clark Co., Lake Mead
M. minutissima (Steud.) Swallen	P&A 3990	USA. Arizona: Coconino Co., W of Flagstaff
	P&A 4048	MEXICO. Chihuahua: 12 mi SW of Madera off Hwy 16 towards Cuauhtemoc
	P&A 4097	MEXICO. Durango: 3.2 mi W of Rio Chico crossing, 22.1 mi W of Durango on Hwy 40
	P&A 4515	MEXICO. Chuhuahua: 9.1 mi E of Cumbres de Majalca
M. montana (Nutt.)Hitchc.	P,A&H 8033	MEXICO. Chihuahua: 25.6 mi S Creel on road to Batopilas
	P&KI 8214	MEXICO. Chihuahua: 33.7 mi W La Junta on road to Parque Nacional Cascada de Basaseachic
	P&CV 9733	MEXICO. Oaxaca: 4.8 mi NW Tlaxiaco on road to San Juan Mixtepec

TAXON	COLLECTORS	LOCALITY
	P&A 9971	MEXICO. Tlaxcala: 5.2 mi N Tlaxco on Mex 119 to Zacatlan
	P&Kl 8171	USA. Arizona: Cochise Co., 10 mi W Portal on F542, E of Onion Pass
	P&A 5438	USA. Arizona: Santa Cruz Co. Patagonia Mts., 12.3 mi S Patagonia on Forest Service Road 49
M. mucronata (Kunth) Trin.	P&A 10778	MEXICO. Chuhuahua: 40 mi W of Balleza and 19 mi E of Guachochi
M. mutica (Rupr. ex E. Fourn.) Hitchc.	A.S. Hitchcock 6348	MEXICO. Veracruz: Orizaba
M. nigra Hitchc.	P&A 11081*	MEXICO. Mexico: 28.3 mi NE Temascaltepec on Mex 134 towards Toluca
M. orophila Swallen	P&A 11105	MEXICO. Mexico: 15.6 mi E Amecameca and 2 mi N Paso de Cortes
M. palmeri Vasey	P&Kl 8322	MEXICO. Tamaulipas: 63 mi SW Cd. Victoria on Mex 101 towards San Luis Potosi
	P&A 11134	MEXICO. San Luis Potosi: 45 mi NE San Luis Potosi on road towards Guadalcazar
	P&A 5478	USA. Arizona: Cochise Co., 3.1 mi above Upper Picnic Area, Fort Huachuca Military Reservation
	P&A 5681	USA. Arizona: Pima Co., Santa Rita Mts. Box Canyon, 7 mi W Hwy 83 on Forest Service Road 62
M. palmirensis Grignon & Laegaard	P,A&PO 8810	ECUADOR. Provincia de Chimborazo: 8.9 km N Palmira on the Panamerican Hwy
M. pauciflora Buckley	P&A 5715*	USA. Texas: Culberson Co., Guadalupe Mts., Pine Springs on Hwy 62 (180)
M. peruviana (P. Beauv.) Steud.	P&J 9308	ECUADOR. Provincia Cotopaxi: Lago Limpiopunga
	P&A 4071	MEXICO. Durango: 14 mi SW of El Vergel on Hwy 24
	P&A 4125	MEXICO. Durango: 7.0 mi W of El Salto on Hwy 40
M. pilosa P.M. Peterson, Wipff & S.D. Jones	P&A 11061	MEXICO. Mexico: 5 km NE of Tejupilco on Mex 134 towards Temascaltepec
M. plumbea (Trin.)Hitchc.	P,A&V 10765	MEXICO. Chihuahua: 35 mi W Balleza and 24 mi E Guachochi
M. polycaulis Scribn.	P&A 5406, 5407	USA. Arizona: Santa Cruz Co. Patagonia Mts., along road to Red Mt., 7.6 mi SE of Patagonia
	P,A&V 10764	MEXICO. Chihuahua: 35 mi W Balleza and 24 mi E Guachochi
M. porteri Scribn. ex Beal	P&Kl 8144	MEXICO. Chihuahua: 17 mi S of Nuevo Casas grandes on Mex 2
M. pubescens (Kunth) Hitchc.	P,D,B&K 13440	MEXICO. Durango: 4.5 mi N of Borbollones, N of Hwy 40
M. pubigluma Swallen	P&A 10593, 10594	MEXICO. Coahuila: 85.5 mi NW of Muzquiz on Hwy 53 towards Boquilla del Carmen
	P&K 13329*	MEXICO. Nuevo Leon: 6.7 mi W 18 de Marzo up road towards Cerro del Potosi

TAXON	COLLECTORS	LOCALITY
M. pungens Thurb. ex A. Gray	P&A 5614	USA. Arizona: Apache Co., 20 mi N St. Johnson Hwy 666 (61)
M. purpusii Mez	P&Kl 8325	MEXICO. Tamaulipas: 63 mi SW Cd. Victoria on Mex 101 towards San Luis Potosi
M. quadridentata (Kunth) Trin.	P&A 6009	MEXICO. Durango: 40 km W Durango on Hwy 40, and 6 mi W Rio Chico
	P&A 11082	MEXICO. Mexico: 28.3 mi NE of Temascaltepec on Mex 134 towards Toluca
	H&C 906 (CIIDIR)	MEXICO. Mexico: Parque Nacional Nevado de Toluca
	H&C 899 (CIIDIR)	MEXICO. Oaxaca Ladera SW del Cerro Pelon, 500 m antes del mirador
	H&C 917 (CIIDIR)	MEXICO. Puebla: Ladera E del Popocatepetl, 10 km W de Santiago Salicintla
M. racemosa (Michx.) Britton, Sterns & Poggenb.	M.W. Talbot 814	USA. New Mexico: Santa Fe Co., Santa Fe Canyon
M. ramosa (Hack. ex Matsum.) Makino	S&P 5302	CHINA. Kiangwang Shan: ca 15 km E of Dongchuan, ca 120 km NNE of Kunming
M. ramulosa (Kunth) Swallen	P&A 4109, 4113	MEXICO. Durango: W of Navios
	P&A 4121	MEXICO. Durango: W of El Salto
	P&A 4621	MEXICO. Michoacan: E of Opopeo
M. reederorum Soderstr.	P&A 6026	MEXICO. Durango: 56 km W Durango,on Hwy 40
	P,G&K 13643	MEXICO. Durango: 6 mi S Charcos on road towards San Juan de Michis
	P,D,B&K 13408	MEXICO. Sinaloa: 3 mi SW Estado de Durango and 2.2 mi S El Palmito on Hwy 40
M. repens (J. Presl) Hitchc.	P&A 5422	USA. Arizona: Santa Cruz Co. Patagonia Mts., junction of Forest Service Road 135 & 49
M. reverchonii Vasey & Scribn.	P&A 6273	USA. Texas: Bexar Co. 5 mi N of San Antonio, city limits on Hwy 281
M. richardsonis (Trin.) Rydb.	P&A 4056	MEXICO. Chihuahua: 10 mi W of Cuahutemoc on Hwy 16
M. rigens (Benth.) Hook.	P&A 8110	MEXICO. Chihuahua: 5.6 mi N Cuahutemoc on Mex 23
	P&Kl 8238	MEXICO. Chihuahua: 76 mi W La Junta in Parque Nacional Cascada de Basaseachic
	P,A&V 10870	MEXICO. Chihuahua: 52.5 mi SE Villa Matamoros and 1 mi N Ejido Revolucion
M. rigida (Kunth) Trin.	P,A&PO 8895	ECUADOR. Provincia de Azuay: 17.7 km N Ona on the Panamerican Hwy
	P,A&PO 8820	ECUADOR. Provincia de Chimborazo: 8.7 km W Alausi on road to Sibambe
	P&Kl 8187	MEXICO. Chihuahua: 44.5 mi SE Madera on Mex 16 and 1 mi S Temosachic
	P&K 13300	MEXICO. Nuevo Leon: 13.4 mi E Hwy 57 on Hwy 58 at crossin Rio Potosi
	P&K 13301*	MEXICO. Nuevo Leon: 13.4 mi E Hwy 57 on Hwy 58 at crossin Rio Potosi
	P&Kl 8316	MEXICO. Tamaulipas: 63 mi SW Cd. Victoria on Mex 101 towards San Luis Potosi

TAXON	COLLECTORS	LOCALITY
	P&CV 9707	MEXICO. Oaxaca: 6.5 mi NE Villa de Tamazulapan and 2 mi NE Teotongo
	P&CV 9728	MEXICO. Oaxaca: 5 mi SW Teposcolula and 2.5 mi NE Yolomecatl on Mex 125
	P&A 5455	USA. Arizona: Cochise Co., 2 mi SW Sunnyside along Forest Service Road 228
	P&A 5434	USA. Arizona: Santa Cruz Co. Patagonia Mts., 12.3 mi S Patagonia on Forest Service Road 49
M. robusta (E. Fourn.) Hitchc.	P,G&K 13594	MEXICO. Mexico: Durango: 5 mi E of Mezquital on road to Charcos
M. schmitzii Hack.	P&A 4631	MEXICO. Michoacan: 6.1 mi W of Ciudad Hidalgo on Hwy 15
M. scoparia Vasey	P&A 6079	MEXICO. Nayarit: 29 mi SW of Tepic on Hwy 15 to Guadalajara
M. schreberi J.F. Gmel.	P 14231*	USA. Maryland: Montgomery Co. Bethesda, 4520 Cheltenham Dr.
M. seatoni Scribn.	P&A 9946	MEXICO. Puebla: 3.5 mi SE Cd. Serdan on Mex 140
M. setarioides E. Fourn.	P&CV 9897	MEXICO. Oaxaca: 1.4 mi E Ayutla on Mex 179 towards Mitla
M. setifolia Vasey	P&K 13376	MEXICO. San Luis Potosi: 2.5 mi E Hwy 57 on road towards Guadalcazar
	P&A 5716	USA. Texas: Culberson Co., Guadalupe Mts., Pine Springs on Hwy 62 (180)
M. sinuosa Swallen	P&A 12590	MEXICO. Chihuahua: Sierra El Nido, 16.7 mi W of Hwy 45 on road up Los Prietos Canyon
M. sobolifera (Muhl. ex Willd.) Trin.	C.H. Bissell s.n.	USA. Connecticut: Rocky woods near Savage St.
M. speciosa Vasey	P,G&K 13626	MEXICO. Durango: 7 mi SE of Mezquital on road to Charcos
	P,D,B&K 13409	MEXICO. Sinaloa: 3 mi SW Estado de Durango and 2.2 mi S El Palmito on Hwy 40
M. spiciformis Trin.	P&A 6244	MEXICO. Coahuila: approx. 20 mi SE Saltillo on road to Los Lirios
	P&Kl 8334	MEXICO. Nuevo Leon: 3.8 mi S Allende on Mex 85 towards Montemorelos
	P&A 9896	MEXICO. Oaxaca: 1.4 mi E Ayutla on Mex 179 towards Mitla
	P&A 9945	MEXICO. Puebla: 3.5 mi SE Cd.Serdan on Mex 140
	P&A 10590	MEXICO. Coahuila: 85.5 mi NW Muzquiz on Hwy 53 towards Boquilla del Carmen
	P&Kl 8332	MEXICO. Tamaulipas: 55 mi SW Cd. Victoria on Mex 101 towards SanLuis Potosi
M. straminea Hitchc.	R. Endlich 1210	MEXICO. Chihuahua.
M. stricta (J. Presl) Kunth	P 13709	MEXICO. Jalisco: 8.2 mi NW Cuautla on road towards Los Volcanes
	P&Kl 8324	MEXICO. Tamaulipas: 63 mi SW of Ciudad Victoria on Mex 101 to San Luis Potosi
M. strictior Scribn. ex Beal	P&A 4520	MEXICO. Chihuahua: 21.1 mi W of Hwy 45, 0.4 mi E of Cumbres de Majalca
	P&A 4039	MEXICO. Chihuahua: 3.1 mi S of Hernandez Javales, 32 mi SW of Colonia Juarez
	P&A 4054	MEXICO. Chihuahua: 15.5 mi W of La Junta on road to Tomochic

TAXON	COLLECTORS	LOCALITY
	P&A 4098	MEXICO. Durango: 2.1 mi W of Rio Chico crossing, 21 mi W of Durango on Hwy 40
M. subaristata Swallen	F.W Pennel 18572	MEXICO. Durango: El Salto (aserradero)
M. sylvatica (Torr.) Torr. ex A. Gray	C.A. Weatherby 5139	USA. Connecticut: Stafford
M. tenella (Kunth) Trin.	P&A 4618	MEXICO. Michoacan: S of Uruapan on Mex 37
	P&A 4755	MEXICO. Nayarit: 10.2 mi W of Tepic on road to Miramar
M. tenuiflora (Willd.) Britton, Sterns & Poggen.	Ch.C. Deam 46,172	USA. Indiana: Noble Co., 5 mi SE of Albion
M. tenuifolia (Kunth) Trin.	P&A 4513	MEXICO. Chihuahua: 0.7 mi W of Nuevo Majalca, 8.5 mi W of Hwy 45
	P&A 8104	MEXICO. Chihuahua: 54.4 mi N Parral on Mex 24 to Chihuahua
	P&A 4059	MEXICO. Chihuahua: 3 mi NE of Parral on Hwy 45 towards Chihuahua
	P&A 4062	MEXICO. Chihuahua: 15.6 mi NE of El Vergel on Hwy 24
	P&A 4092	MEXICO. Durango: 21 mi of Rio Chico, 21 mi W of Durango on Hwy 40
	P&A 10514	USA. Texas: Jeff Davis Co., 7.5 mi SW Hwy 118 on Hwy 166, NE Valentine
M. tenuissima (J. Presl) Kunth	P&A 4751	MEXICO. Jalisco: 2 mi NW of Magdalena on Mex 15 and 15 mi from Guadalajara
M. texana Buckley	P 9613	MEXICO. Chihuahua: 10 mi SW La Junta on road to Creel
	P&A 4545	MEXICO. Chihuahua: Cascada de Basaseachic, 37 mi W of Tomochic, 0.6 mi from overlook
	P&A 4045	MEXICO. Chihuahua: 5.0 mi S of Hernandez Javales
	P&A 4019, 4021	USA. Arizona: Santa Cruz Co., 7 mi SW of Canelo on Hwy 83
M. thurberi (Scribn.)Rydb.	P&A 5618	USA. Arizona: Apache Co., Antelope House Overlook, N rim above Canyon del Muerto
	P&A 5619	USA. Arizona: Apache Co., Antelope House Overlook, N rim above Canyon del Muerto
	P&A 7870	USA. New Mexico: Rio Arriba Co., on Hwy 84, at Echo Amphitheater
M. torreyana (Schult.) Hitch.	P&L 8480	USA. New Jersey: Burlington Co., 0.1 mi N of Atlantic/ Burlington Co. lines on Hwy 206
M. torreyi (Kunth) Hitchc. ex Bush	P,A&M 10208	ARGENTINA. Provincia Salta: 48 km E of Cachi on Hwy 40 to Salta
	P&A 11364	ARGENTINA. Mendoza; San Carlos: near Estacion Arroyo Hondo on junctn road Hwy 40 & variant 40
	P&A 11418	ARGENTINA. Mendoza; Depto. Lujan de Cuyo: approx. 21 km SW Potrerillos on road toward San Jose

TAXON	COLLECTORS	LOCALITY
	P&A 11621	ARGENTINA. Tucuman; Depto. Tafi del Valle: 30 km SE Amaicha de Valle & 25 km NW Tafi del Valle
	P&A 11701	ARGENTINA. Salta; Depto. Chicoana: just E Piedra del Molino on Hwy 33 between El Carril and Cachi
	P&A 11726	ARGENTINA. Salta; Depto. San Carlos: 3 km S Isonza and 23 km N Amblayo
	P&A 5549	USA. New Mexico: Grant Co., 12 mi E Central on Hwy 90
M. uniflora (Muhl.) Fernald	J.V. Haberer 3266	USA. New York: Oneida Co., Forestforth
M. utilis (Torr.) Hitchc.	P&A 6259	MEXICO. Coahuila: 8 mi E of Los Lirios on road to Laguna de Sanchez
M. vaginata Swallen	P&A 4070	MEXICO. Chihuahua: 0.5 mi NE of El Vergel
	P&A 4111	MEXICO. Durango: 5.4 mi W of Navios, 42 mi W of Durango on Hwy 40
	P&A 4124, 4591	MEXICO. Durango: 7.0 mi W of El Salto on Hwy 40
M. versicolor Swallen	P&A 11053	MEXICO. Mexico: 1.1 mi N Tejupilco on Mex 134 towards Temascaltepec
M. villiflora Hitchc. var. *villiflora*	P&A 6228	MEXICO. San Luis Potosi: 10.3 mi NW Matehuala on road to Cedral, near Km marker 12
M. villiflora var. *villosa* (Swallen) Morden	J.R. & C.G. Reeder 4536	USA. Texas: Glasscock Co., 15 mi S of Stanton
M. virescens (Kunth) Kunth	P&A 5876	MEXICO. Chihuahua: 15 mi S San Juanito & 3 mi N Creel
	P&A 5589	USA. New Mexico: Catron Co., 2.1 mi E Hwy 180 on Forest Service Road 35, San Francisco Mts.
M. virletii (E. Fourn.) Soderstr.	P,D,B&K 13429	MEXICO. Durango: 2.4 mi N Borbollones, N Hwy 40
	P&CA 9709	MEXICO. Oaxaca: 10 mi NE Villa de Tamazulapan and 5.5 mi NE Teotongo
	P&CA 9723	MEXICO. Oaxaca: 2.6 mi E Teposcolula on Mex 125
	P&CA 9724	MEXICO. Oaxaca: 2.6 mi E Teposcolula on Mex 125
	P&CA 9729	MEXICO. Oaxaca: 5 mi SW Teposcolula and 2.5 mi NE Yolomecatl on Mex 125
M. watsoniana Hitchc.	Hernandez s.n. (HUAA)	MEXICO. Aguascalientes: San Jose de Gracia, Sierra Fria
M. wrightii Vasey ex J.M. Coult.	P&A 5592	USA. New Mexico: San Francisco Mts., Potato Patch, 3 mi E Hwy 180 on Forest Service Road 35
	P 9586	MEXICO. Chihuahua: 13 mi W Cuahutemoc on Mex 16
M. xanthodas Soderstr.	Hernandez & Sharp 311	MEXICO. Chiapas: Between Escuipulas and Cañada Honda

APPENDIX 2.
Data set used in the cladistic analysis.

Eragrostis acutiflora	2[12]111221221112[23]2
Erioneuron avenaceum	1211111111121232
Leptochloa virgata	[12]1231221222212322
Sporobolus airoides	3[24]33232211212322
M. aguascalientensis	2121111111111322
M. alamosae	[12]13212212211222
M. andina	2121122122111232
M. angustata	3231231211123[12]1
M. annua	1111121111121132
M. appressa	[12]11112212211132
M. arenacea	21111111111121[12]22
M. arenicola	21111111111122[12]22
M. argentea	21211111111212[23]2
M. arizonica	2111111111121132
M. arsenei	1121122121111 2[23]2
M. asperifolia	2111111111111 2[23]2
M. articulata	[23]23113121111 2322
M. aurea	2[24]231112112 12322
M. brandegei	[12]11112212211132
M. brevifolia	2111111111111122
M. breviligula	2[24]33111211212322
M. brevis	111[12]121111211[23]2
M. breviseta	21111211111111[23]2
M. brevivaginata	2[14]21111111111212
M. bushii	1121122122111232
M. californica	1121122122111132
M. capillaris	2[24]3111[12]211112[23][23]1
M. capillipes	1121121111111132
M. caxamarcensis	21111111111111[12]2
M. ciliata	11111221221111[23]2
M. cleefii	2111111111111122
M. crispiseta	[12]11112111112 1122
M. cualensis	1121111111111322
M. xcurtisetosa	1121122122111232
M. curtifolia	21211221 2[12]121322
M. curviaristata	11231221221212[23]2
M. curvula	[23][14]21111111111322
M. cuspidata	2111111111121232
M. depauperata	2111121111121132
M. distans	2[24]2[23]111211222322
M. distichophylla	2[24]23111211212322
M. diversiglumis	1111122122111132
M. dubia	3231231211112311
M. dumosa	1121122122111132
M. durangensis	1121231111111222
M. elongata	2[24]31111111112322
M. eludens	[12]11112111112 11[23]2
M. emersleyi	[12]41311121121 2322
M. eriophylla	2121111111111[23]22
M. expansa	[23]43111121111 2322
M. fastigiata	2111111111111132
M. filiculmis	[23][14]1111111111[23][23]2
M. filiformis	2111121111111132
M. filipes	[23]43111121111 2322
M. flabellata	1121111111111222
M. flavida	[12]111121111111[23]2
M. flaviseta	21211111111 21[23]22
M. flexuosa	2111111111121222
M. fragilis	[12]11112111112 1132
M. gigantea	2433111211212222
M. glauca	11111 2[12]12[12]111132
M. glabriflora	1121122122111132
M. glomerata	1121122122111132
M. grandis	2[24]23111211212322
M. gypsophila	3231231211112311
M. hakoensis	1123122122121222
M. himalayensis	1123122122121222
M. hintonii	2121111111111322
M. huegelii	11221221221 21[12]22
M. implicata	2111121111111112
M. inaequalis	2423111211212322
M. xinvoluta	2433111211212322
M. iridifolia	2[24]23111211212322
M. jaime-hintonii	24111311111 12[23]22
M. jaliscana	3231231211112311
M. japonica	1123122122121222
M. jonesii	2[14]11111111111[12]2
M. lehmanniana	2[24]23111211222322
M. ligularis	2111121111111132
M. lindheimeri	2423111211212222
M. longiglumis	2[24]331112112 12[23]22
M. longiligula	2[24]2311121[12]212222
M. lucida	3231231211112321
M. macroura	3231231211112311
M. majalcensis	2111121111111132
M. mexicana	11211221221112[23]2
M. mex.var.filiformis	11211221221112[23]2
M. michisensis	2121111111111222
M. microsperma	1111122122111132
M. minutissima	2111121111121132
M. montana	[23][14]311111111[12][23]22
M. mucronata	3231231211112311
M. mutica	2[24]21111211112322
M. nigra	3231231211112311

M. orophila	1111111111111[12]22
M. palmeri	3231231211112321
M. palmirensis	2111111111111122
M. pauciflora	212112212[12]111222
M. pectinata	1111122122111[23]2
M. peruviana	2111121111111132
M. pilosa	2413111211212222
M. plumbea	2111111111112[23]2
M. polycaulis	2111122121111[23]2
M. porteri	2121122122111[12]22
M. pubescens	2[24]2311121121222 2
M. pubigluma	242113121111 2[23]22
M. pungens	2421111111112[23]22
M. purpusii	2221111111112[23]22
M. quadridentata	[23]121111111111322
M. racemosa	1121122122111 2[23]2
M. ramosa	112112212212 1[12][23]2
M. ramulosa	[12]1111211111111132
M. reederorum	2433111211212322
M. repens	2111111111111[23]2
M. reverchonii	2[14]21111111112[23]22
M. richardsonis	2111111111111132
M. rigens	3231231211112321
M. rigida	3231231211112311
M. robusta	2433111211212322
M. scoparia	2[24]2311121121232 2
M. schmitzii	2111121111111132
M. schreberi	1121122122111222
M. seatonii	2111111111111222
M. setarioides	1121122122111222
M. setifolia	2[12]31111111122122
M. sinuosa	2111121111121122
M. sobolifera	2121122122111222
M. speciosa	2[24]231112112 12[23]22
M. spiciformis	21111221221 11[12][23]2
M. straminea	2131111111111322
M. stricta	2431231211112[23]22
M. strictior	1111121111111[12]2
M. subaristata	3231231211112212
M. sylvatica	1121122122111222
M. tenella	1111122122111[23]2
M. tenuiflora	1121122122111222
M. tenuifolia	1111122122111122
M. tenuissima	1111121111111[23]2
M. texana	2111121111121122
M. thurberi	21111221 2[12]111[12]22
M. torreyana	2[24]2311111111[12][23]2
M. torreyi	2111111111122[23]22
M. uniflora	2[14]2111111121[12][12]2
M. utilis	211111111111[12]22
M. vaginata	2111121111111[23]2
M. versicolor	2[24]31111111112[23]22
M. villiflora	2111111111111122
M. vill.var.villosa	2111111111111122
M. virescens	3[12]312111111[12][23]12
M. virletii	2[24]21111111112[23]22
M. watsoniana	212111111121[23]22
M. wrightii	2[14]11111111[12]1122
M. xanthodas	2[24]2311212112 12222

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